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The effect of the Permian mass extinction on shark faunas

The Effect of the Permian Mass Extinction on Shark Faunas

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Abstract

The End-Permian mass extinction was the single largest extinction event in history. The effect of this event on shark faunas is examined herein.

Several new specimens of hybodont are described. *Polyacrodus twitchetti* n. sp. and *Lissodus angulatus* are described from the Lower Triassic of Greenland. Several specimens assigned to *Lissodus* aff. *cassagnesis* and Hybodontiformes indet. are described from the Lower Triassic of Madagascar. Additional specimens are described from the Lower Triassic of the Wapiti Lake area of British Columbia and are assigned to *Wapitiodus wapitiensis* n. gen., n. sp., *Contrariodus wapitiensis,* n. gen, n. sp., *Polyacrodus* sp. and Hybodontiformes indet.

In order to more accurately examine the effects of the event on sharks the genera of the Superfamily Hybodontoidea that occur in the Permian and Triassic are reviewed and the currently accepted diagnostic characteristics are given for each genus. The Family Polyacrodontidae is reviewed in more detail and specimens previously assigned to *Polyacrodus* are re-assigned to either *Polyacrodus, Lissodus* or one of three new genera *Aconcinnodus,* n. gen., *Pseudohybodus,* n. gen. and *Contrariodus* n. gen.

The fossil record of all shark specimens found in the Upper Permian and Lower Triassic is reviewed as is the stratigraphic position of all specimens. Countries from which specimens have been found include the USA, Canada, Brail, Greenland, Spitzbergen, Germany, Turkey, Angola, Madagascar, South Africa, Russia, India,

Pakistan, China and Japan. The taxonomic assignment of various specimens is discussed and several are reassigned.

The effect of the extinction event on various aspects of shark ecology and morphology (including diversity, diet, size variation and habitat) is examined. While not always conclusive, several trends emerge. The survivorship of sharks over the P-Tr boundary is relatively high in comparison to the published figures for other groups. In addition to this, the rapid diversification of the surviving genera in the Olenekian shows that detrimental effects of the event on shark diversity were relatively short lived. The post-extinction fauna consists mainly of sharks with generalist feeding strategies but the presence of specialised taxa in the Olenekian indicates a relatively rapid recovery period. The available evidence suggests that sharks did undergo a substantial reduction in body size from the Permian to the Triassic. Hybodonts returned to pre-extinction sizes by the Olenekian, while eugeneodonts remained smaller in the Olenekian and became extinct immediately thereafter. There is insufficient evidence to suggest whether either marine or freshwater sharks were preferentially selected for in the P-Tr extinction event.

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I would like first of all to thank Gilles Cuny for all his tireless help without which this thesis would never have been finished. I would also like to thank the university of Bristol and the Department of Earth Sciences, not only for their financial support, but also for making my time here both fun and interesting. In particular I would like to acknowledge my supervisor Mike Benton for all his help. Additional thanks go to Emma, Erik, Rachel, Simon, Nick, Madeleine, Thea and the other friends within the department that made life, if not always fun, at least never boring.

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This thesis is dedicated to those that took the incredible risk of funding various aspects of my Ph.D. namely my mother and grandmother. Thanks to both of you and apologies for the terrible return on your investment.

Finally thanks to anyone that put up with my endless demands for more caffeine at numerous and utterly reasonable times of the day.

Authors declaration

" I declare the work in this dissertation was carried out in accordance with the regulations of the University of Bristol. The work is original and except where indicated by special reference in the text and in no part of this dissertation has been submitted for any other degree.

Any views expresses in the dissertation are those of the author and in no way represent those of the University of Bristol.

The dissertation has not been presented to any other University for examination either in the United Kingdom or overseas."

Signed

I am the sole contributor of all work as it appears in this thesis. Chapters 3.1.3.2 and 2.2 have been submitted for publication with me as sole author and Chapter 2.3 has been submitted in an altered (additional non shark specimens) form with Raoul Mutter (with me as first author) making additions to the work contained herein.

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Chapter 1

1.0 Introduction

1.1 General Introduction

Of the so-called "Big Five" mass extinction events the end-Permian event was by far the greatest. Terrestrial life was devastated, with an estimated 70% of terrestrial vertebrate families being wiped out (Maxwell 1989). Marine species extinctions over the end-Permian event were no less impressive, with estimates ranging from a conservative 75% (Hoffman 1986) to 96% (Raup 1979), with the majority of recent workers tending towards the higher estimate.

A great deal of work has been done on the effects of the Permian extinction event on invertebrate families, which suffered to various degrees. Some of the worst-hit groups include bryozoans that suffered only slightly less than corals and echinoderms which were almost completely exterminated. Other groups were less affected by the extinction event. These include species of foraminifera and ostracods whose ability to tolerate low oxygen conditions favoured them. Yet other groups, such as bivalves, were able to fill niches left by other harder-hit groups such as gastropods and actually profit from the extinction event.

Little work has been done, however, on the effects of the Permian mass extinction on marine vertebrates including sharks due to the lack of material and the apparent lack of complete boundary sections. In recent years however, several Lower Triassic sharks have

come to light, most notably those in Canada and Greenland, as well as a number from Madagascar. It was generally assumed (Scaheffer 1973) that fish groups crossed the Permo-Triassic boundary relatively unscathed and that the Early Triassic saw a radiation of many fish groups. This work will examine the extent of the effect of the end-Permian extinction event on sharks in more detail in order to discover if they were indeed as unaffected as previously thought.

1.2 Studied Groups

This work will concentrate on the major groups of Permian and Triassic elasmobranchs without examining other chondrichthyan groups. The major shark groups within the Upper Permian include the eugeneodonts and the xenacanths. Hybodonts were the dominant Triassic shark group and while these compose the bulk of the fossil finds from the study period, ctenacnath and neoseachians as well as other more enigmatic taxa will also be mentioned.

Many of the sharks examined in this work are considered by many to be predominately Palaeozoic despite the fact that they cross the P-Tr boundary (Maisey *et al.* 2004). The first of these groups is the Eugeneodontiformes. First described in 1844, these sharks ranged from the Mississippian to the Triassic and were characterised by amongst other things a dentition of pavement-like teeth with a symphyseal tooth whorl and broadened neurapophysial and haemapophysial elements (with little fusion) in the dorsal lobe of the caudal fin (Schultze and West 1996). The best known eugeneodont

from the Permian is *Helicoprion* found from the USA and Eurasia. Other eugeneodonts considered include *Fadenia* and *Erikodus* from Greenland as well as a number of thus far undescribed specimens from the Wapiti lake area of British Columbia.

The second group of predominantly Palaeozoic sharks studied herein are the Xenacanthiformes. Xenacanths are characterised by, amongst other things, a single spine primitively associated with one expanded dorsal fin. Tooth shape is tricuspid with two lateral main cusps and a more reduced central cusp (Zangerl 1981). The base is drawn out ligually and has "a coronal button on its top and a basal tubercule at its bottom side" (Hampe 1991). These are a group of sharks that has been studied since the mid 1800s by amongst others Agassiz (1833) and Woodward (1889) and that range from the Early Devonian to the Upper Triassic. These sharks have been found in environments ranging from freshwater lakes, through brackish into full marine conditions. Distribution of these animals was widespread with fossils having been found from the USA, South America, Europe, Australia and Asia. Genera of xenacanths studied in this work include *Orthacanthus* from the USA, *Triodus* from India and an unidentified xenacanth from Russia.

The ctenacanths were most widespread in the Carboniferous and while present from the Upper Devonian to the Triassic, they were already in decline during the period under study here, with only very few persisting after the P-Tr event. Again having been studied since the early 1800s (Agassiz 1833) the majority of ctenacanth finds consist of isolated fin spines and teeth. Although relatively primitive (characters include a cleaver-

shaped palatoquadrate, cladodont dentition and absence of calcified ribs) ctenacanths were the first sharks to display certain characters associated with modern forms including the shape of the tribasal pectoral and dorsal fins with basal cartilages (Zangerl 1981). The only ctenacanths considered in this work were found in the Lower Triassic of China and have not been assigned to a genus.

The first of the predominantly Mesozoic shark groups is the Hybodontiformes. Having also been studied since the mid 1800's (Agassiz 1833) these sharks comprise the majority of the fossils considered in this work. Hybodonts were the dominant shark group for much of the Triassic and Jurassic (ranging from the Missisipian to the Cretaceous) and, while they were present in the Palaeozoic, it was only after the P-Tr event that they began to diversify rapidly. Hybodonts had a wide array of tooth morphologies adapted to various diets and behaviours. Characters associated with hybodonts (although not necessarily diagnostic of the group) include teeth with low wide crowns, two dorsal fins supported by spines and basal cartilages and large recurved cephalic spines on males (Cappetta 1987). Hybodonts have been found in a variety of environments both marine and freshwater and on all five continents. Hybodont genera considered include *Hybodus, Acrodus, Lissodus, Palaeobates* and *Polyacrodus*, as well as a number of newly described and unidentified genera.

Neoselachians (the group that contains all modern sharks), while present possibly as far back as the Lower Carboniferous, only became truly widespread and dominant in the Bathonian (Chris Duffin pers. comm. 2005). Neoselachians did experience a

diversification in the Upper Triassic (Cuny and Benton 1999), but their occurrence in the Lower Triassic is sparse with only one confirmed find. Neoselachians are a sister group to hybodonts and are characterised mainly by a triple layered enameloid in their teeth. Specimens have been found in both marine and freshwater conditions, though no freshwater finds have been uncovered in the Triassic or Jurassic, neoselachians probably not diverisifying into these habitats until the Cretaceous (Maisey *et al.* 2004). The only confirmed neoselachian mentioned in this work is *Synechodus* sp. from the Lower Triassic of Turkey.

1.3 New material

The main obstacles to the accurate examination of the effects of the P-Tr event on sharks are a general disagreement over the systematics of certain Lower Triassic shark groups (specifically certain groups of hybodonts) and a lack of available fossils that consist of more than just isolated teeth.

The first problem will be addressed initially with a broad-scale revision of the current state of hybodont systematics in order to clarify the characters used to identify the families genera and species considered within this work followed by an in-depth study of one of the least well defined hybodont families namely the Polyacrodontidae.

In order to reduce the inaccuracies caused by the lack of more complete shark fossils from the study period this work will describe a number of original specimens from

various Lower Triassic localities. The first locality from which fossils will be described is Greenland. Two hybodont sharks are described from this area. The first was found in the Wordie Creek Formation on the east side of Schuchert Dal, southern Jameson Land, East Greenland. The second comes from the Kap Stosch region, East Greenland, in the Early Triassic fish zone 5 (Nielsen 1935), equivalent to the *Proptychites* ammonite zone (Nielsen 1935), which corresponds to the Induan (Tozer 1967). One specimens is described as *Polyacrodus twitchetti,* while the other (although previously grouped with material also assigned to *Polyacrodus*) is assigned to *Lissodus angulatus.*

The Wapiti Lake area of British Columbia has also yielded Lower Triassic shark specimens that will be described in this work. While the area has yielded both hybodont and eugeneodont specimens, only the hybodonts are described (though measurements from the eugeneodonts are used in other sections). The specimens from this area are stored in two separate collections both of which were visited. The first is the University of Alberta in Edmonton and the second in the Royal Tyrell Museum of Palaeontology in Drumheller. The sediments in the Wapiti lake area were deposited in a "relatively shallow-water, deltaic to shallow continental shelf environment, in an initially transgressive (Phroso-like strata), but subsequently regressive (Vega-like strata), sea influenced by turbidity and/or storm generated currents"(Neuman 1992). The specimens were found from the Vega Phroso Member of the Sulphur Mountain Formation. Previously thought to be of Smithian in age, recent studies have shown that the fossils are more likely from the Induan to the Olenekian (Orchard and Tozer 1997). Three genera of hybodonts (including one new genus and one renamed genus) have been found from the

area, *Waitiodus, Contratiodus and Polyacrodus,* as well as several specimens that have not been identified to genus level.

The final area from which fossils will be described is Madagascar. These fossils come from the Middle Sakamena Group (Olenekian) which would have been a warm shallow epicontinental sea with a depth of 200-300m (Beltan 1996). Only one genus (*Lissodus*) is described from the area along with a number of Hybodontiformes indet.

1.4 Aims

The study of the effects of the end- Permian event on sharks will be concentrated on four major areas to determine whether there was any selectivity or visible trends in the recovery pattern. These four areas are diversity and distribution, size variation, diet and habitat.

The diversity of sharks will first be considered on a regional scale. In order to consider regional changes, all shark fossil finds from the period will be gathered and organised first geographically by continent and country and then chronologically. Countries in which Upper Permian and Lower Triassic fossil have been found include the USA, Canada, Brazil, Greenland, Spitzbergen, Germany, Turkey, Angola, Madagascar, South Africa, Russia, India, Pakistan, Armenia, China and Japan. This section will include a review of the stratigraphy of each area. Diversity of sharks over the P-Tr boundary will then be considered on a global scale. This section will focus on large-scale

changes and turnover of families, genera and species. Examining the total effect of the P-Tr mass extinction as well as the local effects will allow the analysis of the relative impact the event had on sharks in comparison to the other groups. Factors affecting this section include the tendency of some workers to over-split shark taxa as well as a lack of agreement on characters within certain groups. To that end all finds will be considered and several genera and species will be reassigned.

One of the many suggested consequences of the Permian mass extinctions is the so-called "Lilliput effect" (Urbanek 1993). The Lilliput effect manifests itself as a marked reduction in size of flora and fauna following a major disturbance event such as a mass extinction. It has been postulated that this reduction in size is as a result of a decline in primary productivity (Twitchett 2001). The effects of size will be considered only on a global scale. To this end all measurements of all fossil shark specimens from the study period that consist of more than isolated teeth (i.e. specimens from which size estimates can be made) will be gathered and the tends in size change will be examined and plotted in order to discover if size played any role the P-Tr event either in selectivity or subsequent recovery.

Feeding habits will be also be considered to determine the extent of the influence the had on selectivity and recovery over the P-Tr boundary. While there are a wealth of different shark tooth morphologies over the study period, the examination of dietary habits will group shark dentitions into types In order to examine the wider effects of diet as opposed to the effects on individual families. The dentition types that will be

considered are; piscivorous (tearing and cutting teeth, i.e. feeding mainly on fish), generalist (suited to clutching a variety of prey, i.e. lower crowned and capable of feeding on both fish and soft shelled organism) and finally durophagous (crushing and grinding dentitions, i.e. feeding on hard shelled prey).

Sharks from the Upper Permian and Lower Triassic have been found from a variety of palaeoenvironments ranging from completely freshwater through various deltaic environments to exclusively marine. The extent to which the sharks from various environments were affected remains little a studied yet potentially crucial field. Several workers have suggested that organisms from marine environments suffered less than their freshwater counterparts during mass extinction events (McGhee 1996) though the available evidence for these claims appears to be sparse. Padian and Clements (1985) carried out research on a number of groups including amphibians and bony fish and suggested that freshwater fish and amphibians were less affected than those from marine environments. They also speculated that sharks, being a predominately marine group, suffered relatively more in the P-Tr event but did not perform any in depth examination of various shark groups. Examining the environments from which all Upper Permian and Lower Triassic sharks have will help us to discover whether marine sharks were more adversely affected than those from freshwater habitats.

1.5 Terminology

The terminology used in the descriptions on the skeletal tissue is the same as that used in Maisey (1982). Terminology employed in the description of the teeth that may require clarification includes:

principal/main cusp = largest cusp usually located between sets of flanking smaller cusps.

lateral cusps = smaller cusps located on either side of the main cusp

ridges = elevated lines descending the crown that may or may not bifurcate crown shoulder,

labial / lingual projection/peg = projection on either the labial or lingual face of the crown which is confluent with the main cusp

longitudinal occlusal crest = crest at the apex of the crown running mesio-distally forming a cutting blade

node = projection on either the labial or lingual face of the crown that in not confluent with the main cusp

crown base = the lower extremity of the crown

specialized foramina = foramin on the face of the root that show a clear pattern and orientation.

2.1. Lower Triassic hybodonts from Greenland

2.1.1 Introduction

Two hybodont sharks are described from the Lower Triassic of Greenland. The first hybodont is assigned to *Polyacrodus twitchetti*. The specimen was found in the Wordie Creek Formation on the east side of Schuchert Dal, southern Jameson Land, East Greenland. This is called "section X" in Perch-Nielsen et al. (1972). The concretion was found loose in scree, but could only have come from one of the three concretion horizons near the top of the section (Fig. 2.1). Only one of these has yielded fish remains from in-situ concretions, making it the most likely layer to have contained the specimen (Twitchett et al. 2001). The specimen comes from the *Hindeodus parvus* conodont zone, the basal conodont zone of the Triassic (Yin 1994). The specimen was associated with small ophiceratid ammonoids. In addition to the species description the specimen will be compared to several other genera to identify any possible relationships between them and *Polyacrodus*.

The second species was previously assigned to *Polyacrodus angulatus* but has subsequently been re-identified as *Lissodus angulatus*. The specimen is from the Kap Stosch region, East Greenland (Fig. 2.2), in the Early Triassic fish zone 5 (Nielsen 1935), equivalent to the *Proptychites* ammonite zone (Nielsen 1935), which corresponds to the Induan (Tozer 1967). The Kap Stosch locality encompasses both shallow marine and brackish water palaeoenvironments (Nielsen 1935). The specimen comes from the Pyramiden area located between rivers 8 and 9 (Nielsen 1935).

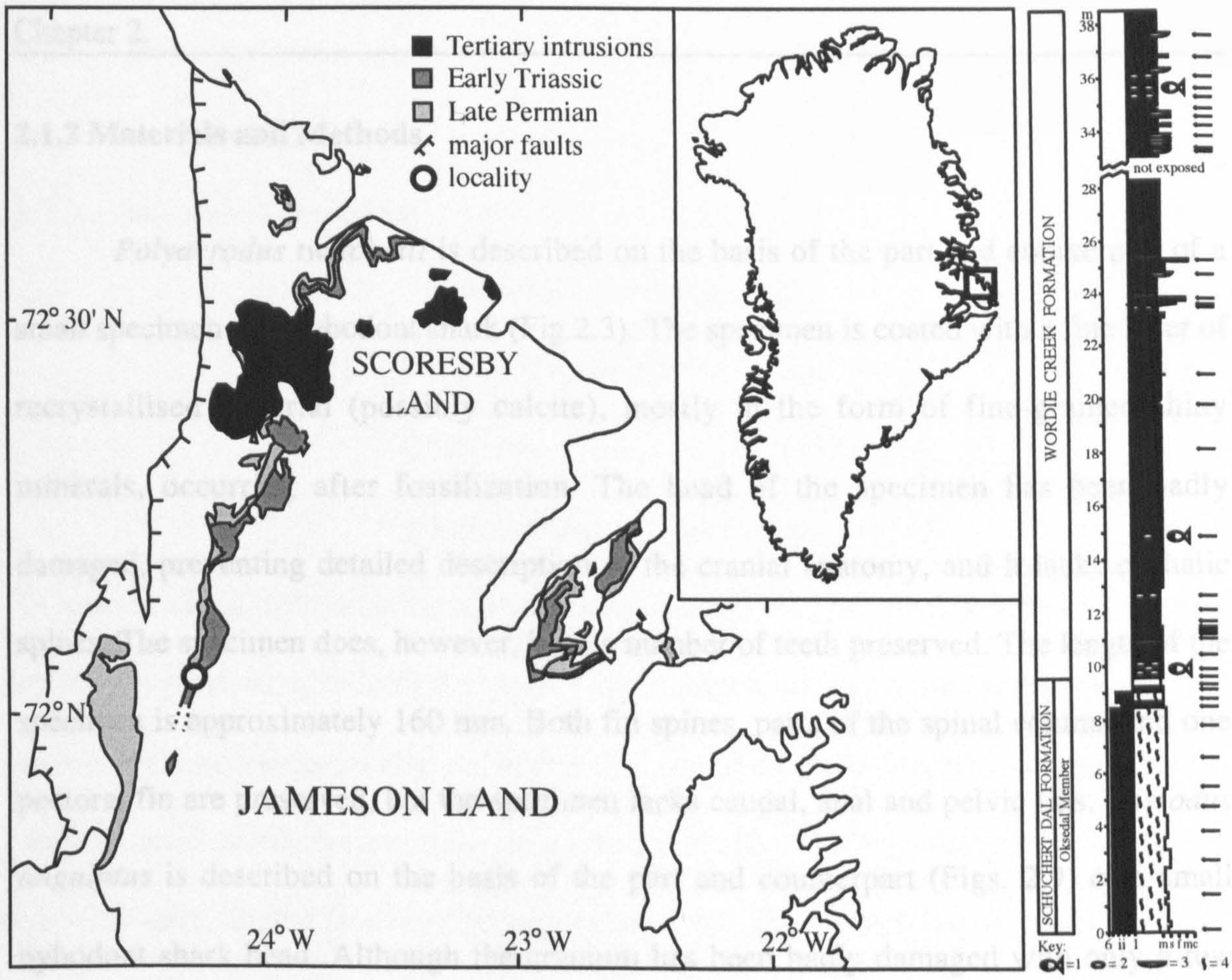


Fig. 2.1. Map of Greenland showing the general location of the Schuchert Dal area and sedimentary log of studied section showing sample horizons (arrowed). ii—ichnofabric index. Symbol key: 1, articulated fish; 2, concretion; 3, gutter cast; 4, bioturbation. Grain-size scale: m, mudstone; s, siltstone; f, fine sandstone; m, medium sandstone; c, coarse sandstone. Reproduced with permission from Twitchett et. al (2001).

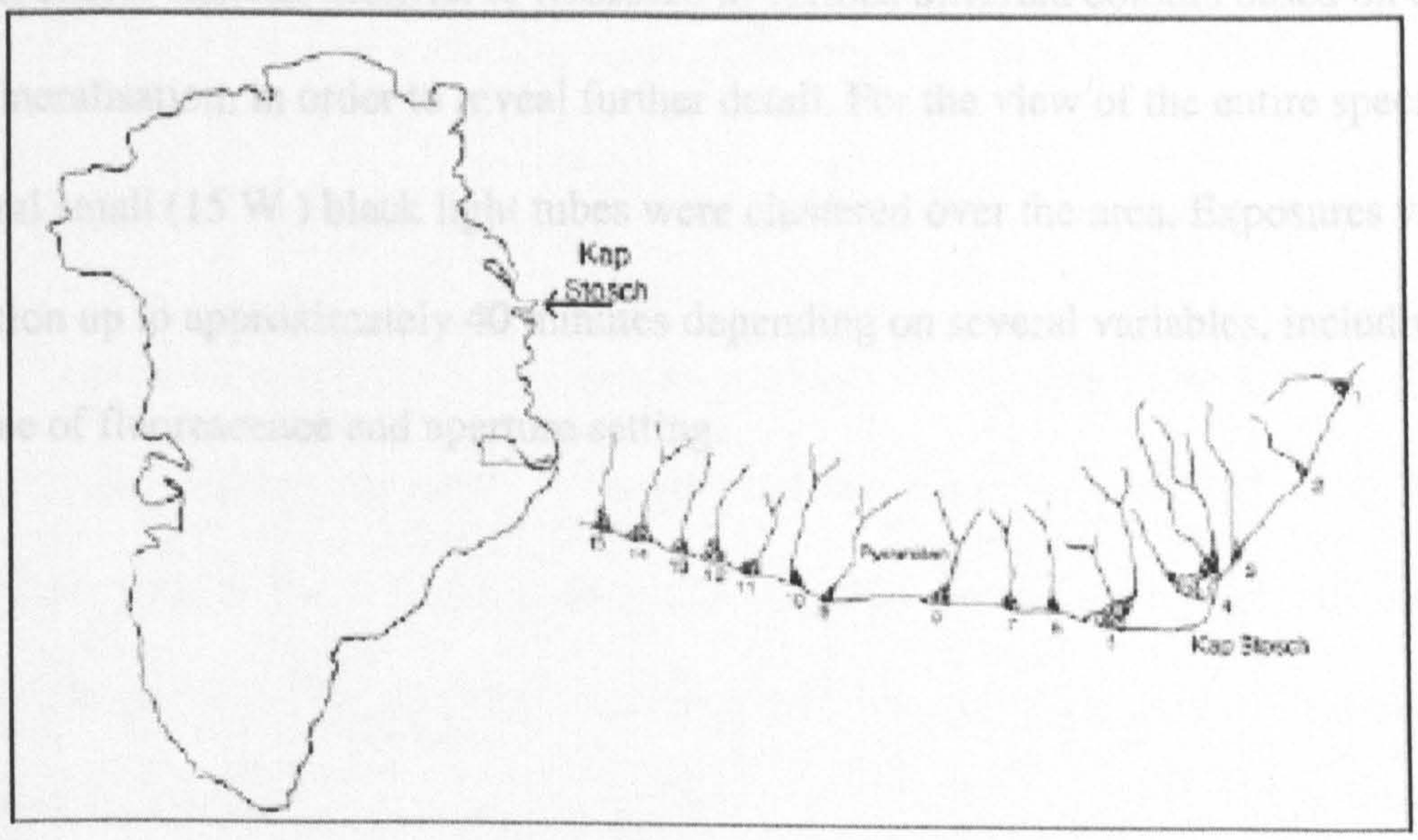


Fig. 2.2. Location of Kap Stosch locality, redrawn from Neilsen (1935).

2.1.2 Materials and Methods

Polyacrodus twitchetti is described on the basis of the part and counterpart of a small specimen of a hybodont shark (Fig.2.3). The specimen is coated with a fine layer of recrystallised material (possibly calcite), mostly in the form of fine-grained shiny minerals, occurring after fossilization. The head of the specimen has been badly damaged, preventing detailed description of the cranial anatomy, and it lacks cephalic spines. The specimen does, however, have a number of teeth preserved. The length of the specimen is approximately 160 mm. Both fin spines, parts of the spinal column and one pectoral fin are preserved, but the specimen lacks caudal, anal and pelvic fins. *Lissodus angulatus* is described on the basis of the part and counterpart (Figs. 2.9) of a small hybodont shark head. Although the cranium has been badly damaged with only a few structures preserved, including a number of teeth, it represents one of the best *Lissodus* heads known to date, and the only known head of *L. angulatus*.

Many of the photographs were taken using low-wavelength ultra violet light, which causes skeletal material to fluoresce in various different colours based on the type of mineralisation, in order to reveal further detail. For the view of the entire specimen, several small (15 W) black light tubes were clustered over the area. Exposures varied in duration up to approximately 40 minutes depending on several variables, including degree of fluorescence and aperture setting.

2.1.3 Systematic Paleontology

2.1.3.1 *Polyacrodus twitchetti*

Cohort Euselachii Hay, 1902

Superfamily Hybodontoidea Owen, 1846

Genus *Polyacrodus* Jaekel, 1889

Polyacrodus twitchetti n. sp.

Diagnosis: Small hybodont shark with a very thin and elongate scapulocoracoid; large mesopterygium; anterior teeth are small ± 1mm; crown low and pyramidal; principle cusp centrally placed mesio-distally and higher than lateral cusps; 1-2 pairs of lateral cusps; three ridges descending from main cusp labially; single ridge descending from lateral cusps labially; lingual face largely unornamented but possessing a lingual peg; root subequal to height of crown. Posterior teeth have a poorly developed main cusp with up to 2 pairs of lateral cusps; each cusp has a single ridge descending from it.

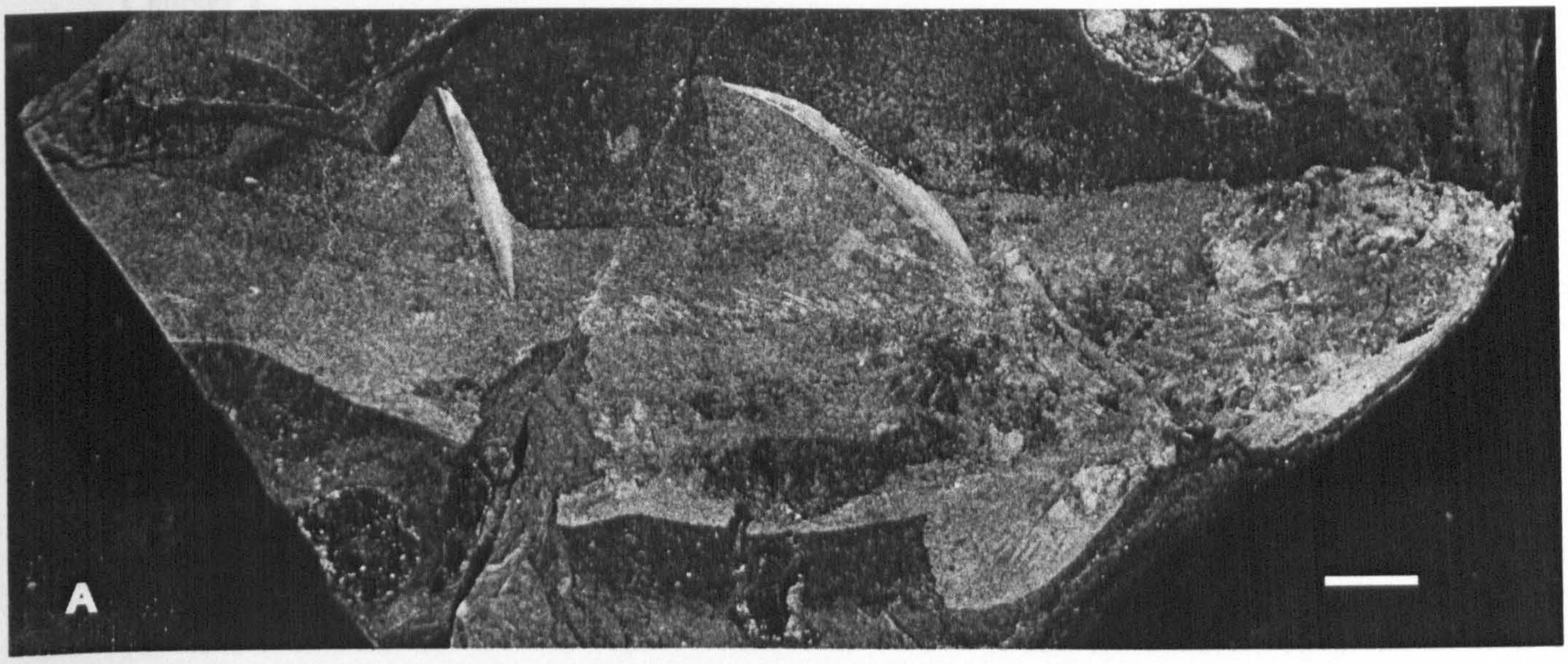
Etymology: Named after the discoverer, Dr. Richard Twitchett (University of Plymouth).

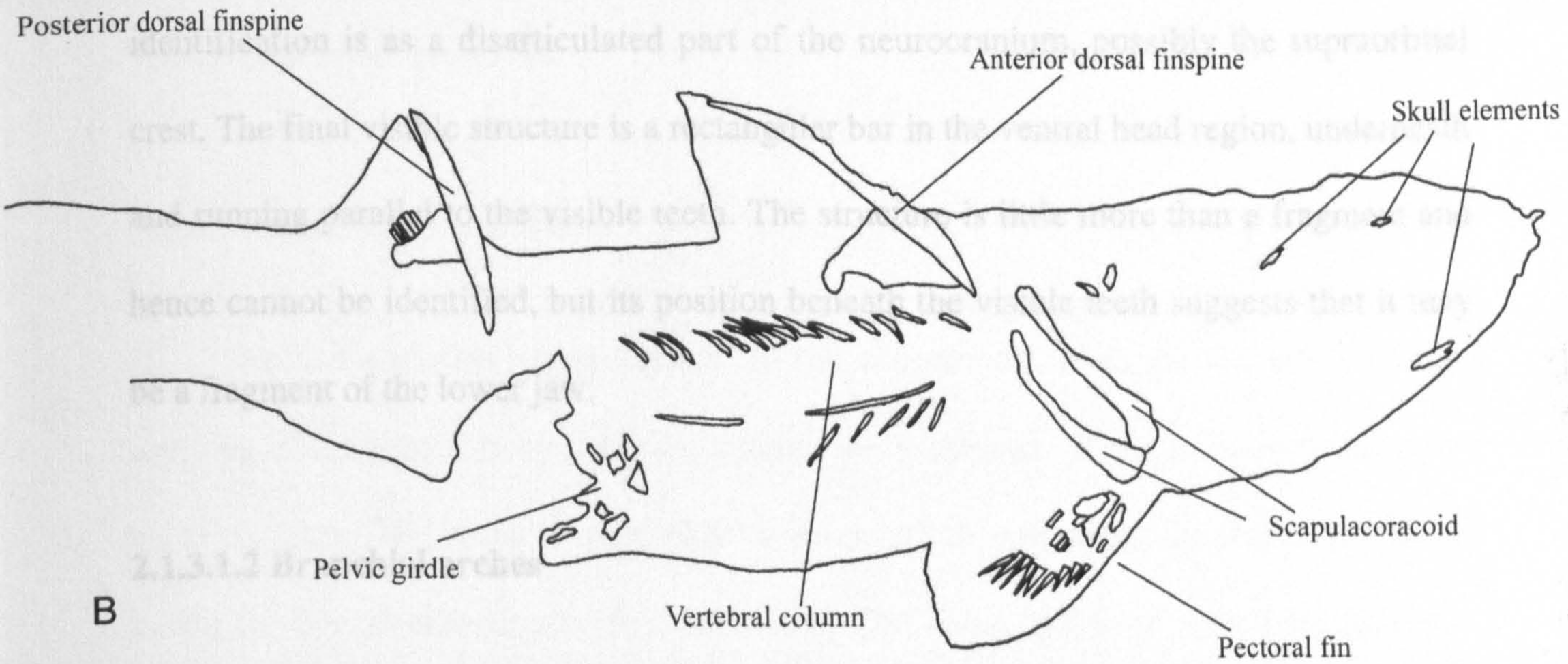
Type Locality : Wordie Creek Formation, Lower Triassic, East Greenland.

Type Specimen: Located at the Copenhagen Geological Museum, V-2006-2.

2.1.3.1.1 Cranial anatomy

As previously stated, the cranial portion of the specimen has been laterally compressed, destroying most of the cranial structure, preventing identification of structures such as the brain case. In addition to this, the secondary recrystallization has masked most of the detail. These factors make interpretation of the visible structures tenuous.





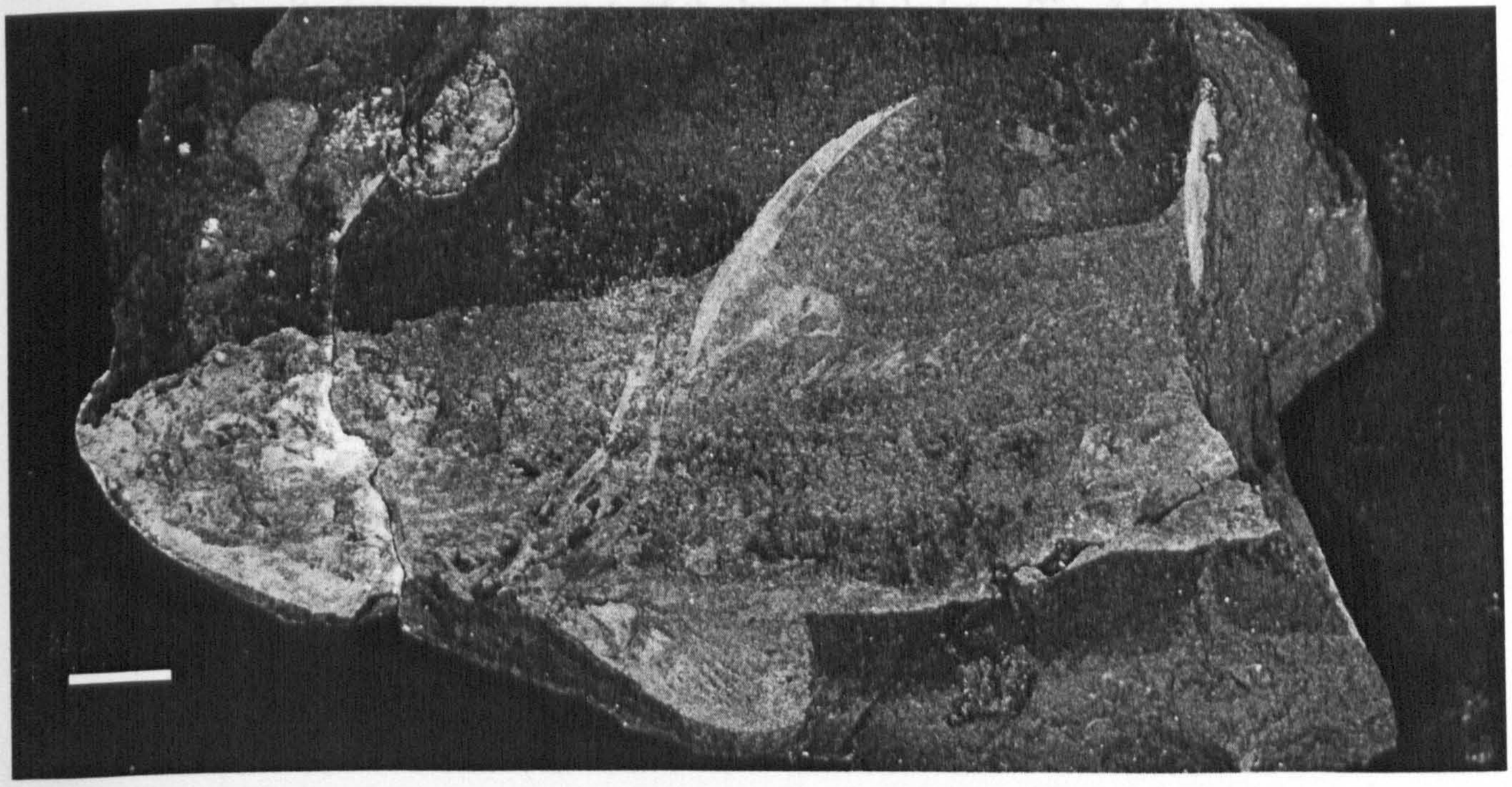


Fig. 2.3. Polyacrodus twitchetti. (A) Part , (B) illustration of part (C) counterpart . Scale bars 10 mm (V-2006-2)

Structures in the anterior region of the head could be part of the neurocranium. Damage to these structures is too extensive to allow reliable identification, but their position indicates that they may be parts of the rostral bar and precerebral fontanelle. A large, slightly curved black structure, located near the center of the head region was thought to be a displaced jaw. However, this seems unlikely due to the lack of teeth and comparison with the visible teeth shows that the structure is far too small. A more likely identification is as a disarticulated part of the neurocranium, possibly the supraorbital crest. The final visible structure is a rectangular bar in the ventral head region, underneath and running parallel to the visible teeth. The structure is little more than a fragment and hence cannot be identified, but its position beneath the visible teeth suggests that it may be a fragment of the lower jaw.

2.1.3.1.2 Branchial arches

Despite damage, some parts of the branchial skeleton (Fig. 2.4) are preserved. As far as can be determined, there are between four and five branchial elements located approximately along the length of the scapulocoracoid. These elements are faintly discernible as anteriorly leaning bars. From the position of the bars relative to the scapulocoracoid, it is likely that the elements are ceratobranchials.

2.1.3.1.3 Vertebral column

The axial skeleton of the specimen consists of neural and haemal elements. These elements are poorly preserved between the occiput and the base of the anterior fin spine, as well as between the base of the posterior fin spine and the end of the preserved section. There are between 19 and 21 posteriorly reclining neural arches between the anterior and posterior fin spines. There are far fewer haemal elements preserved, with only six visible. The rib cage is not preserved.

2.1.3.1.4 Dorsal fins and spines

Both dorsal fins are preserved. In the anterior fin, both the fin spine and fin webbing, distinguishable by dermal denticles, are preserved. There is a single triangular basal cartilage. The spine is inserted at an angle of 46° and at its deepest point almost meets the neural elements of the notochord. The spine has been split longitudinally showing it in cross section with the distal extremity missing but leaving an imprint of its external ornamentation in the matrix. The internal structure shows three layers. The innermost layer is light-coloured and has a fibrous structure, while the outer two layers (the middle one of which is much thinner than the outer mantle) are darker and more solid. The imprint of the outer ornamentation shows evidence of longitudinal ribbing, though preservation is insufficient to make out the fine details of the ornamentation. As well as the ribbing there is evidence of external lesions on the fin spine. These lesions are round and infilled with a lighter calcite-like crystal indicating that the outer ornamentation was stripped away to expose the underlying osteodentine.

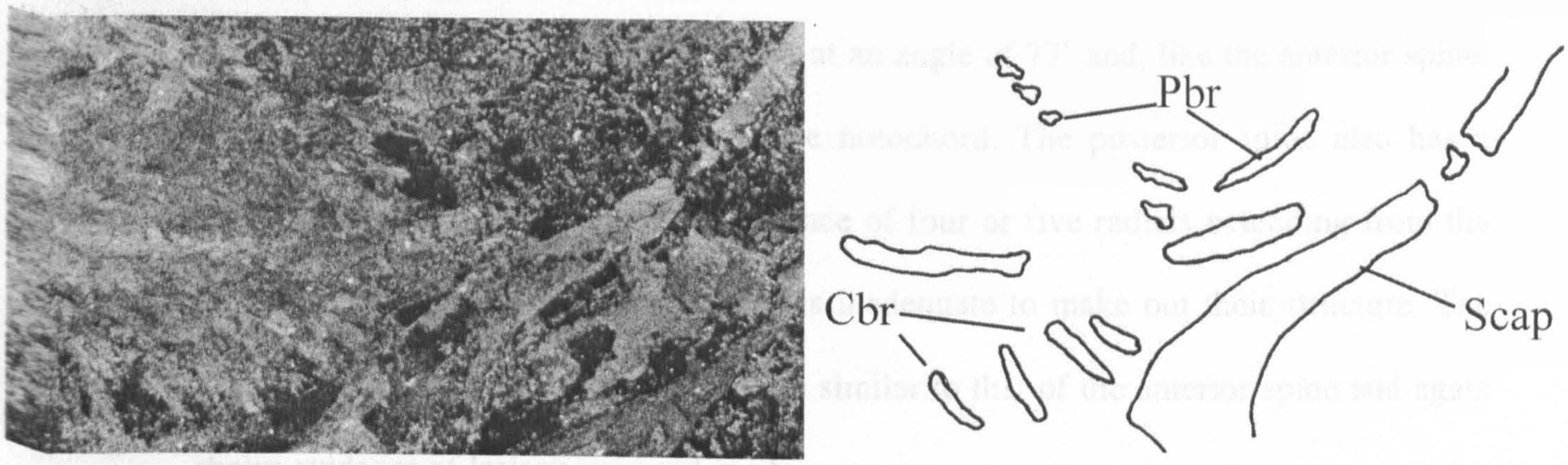


Fig. 2.4. *Polyacrodus twitchetti*. (V-2006-2). Branchial arches. Structure is poorly preserved but several elements are still visible. Pbr = probranchial, Cbr = ceratobrianchial, Scap = scapulocorocoid.

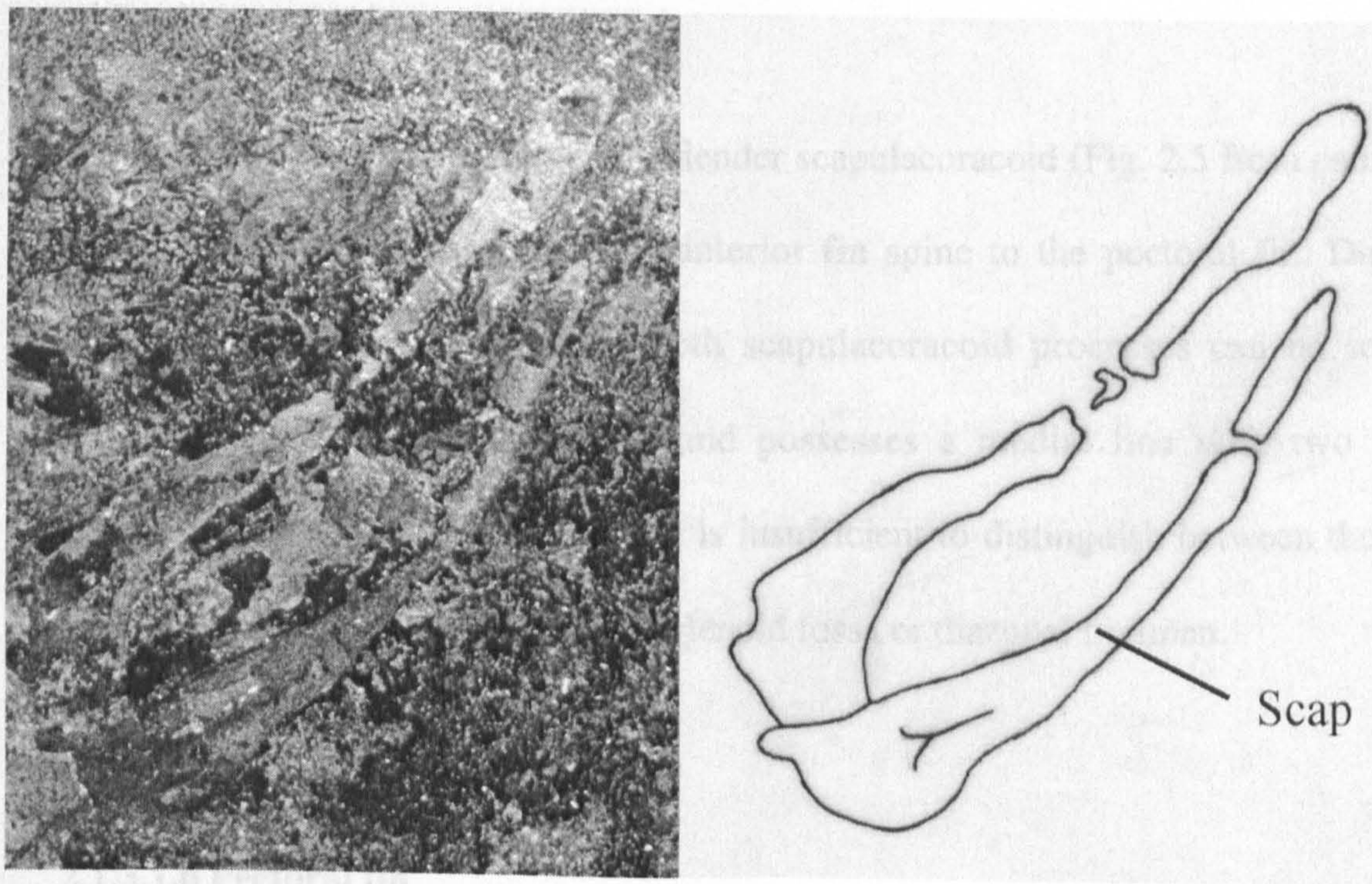


Fig. 2.5. *Polyacrodus twitchetti*. (V-2006-2). Scapulocoracoid. Both halves of long, thin structure visible. Scap = scapulacoracoid

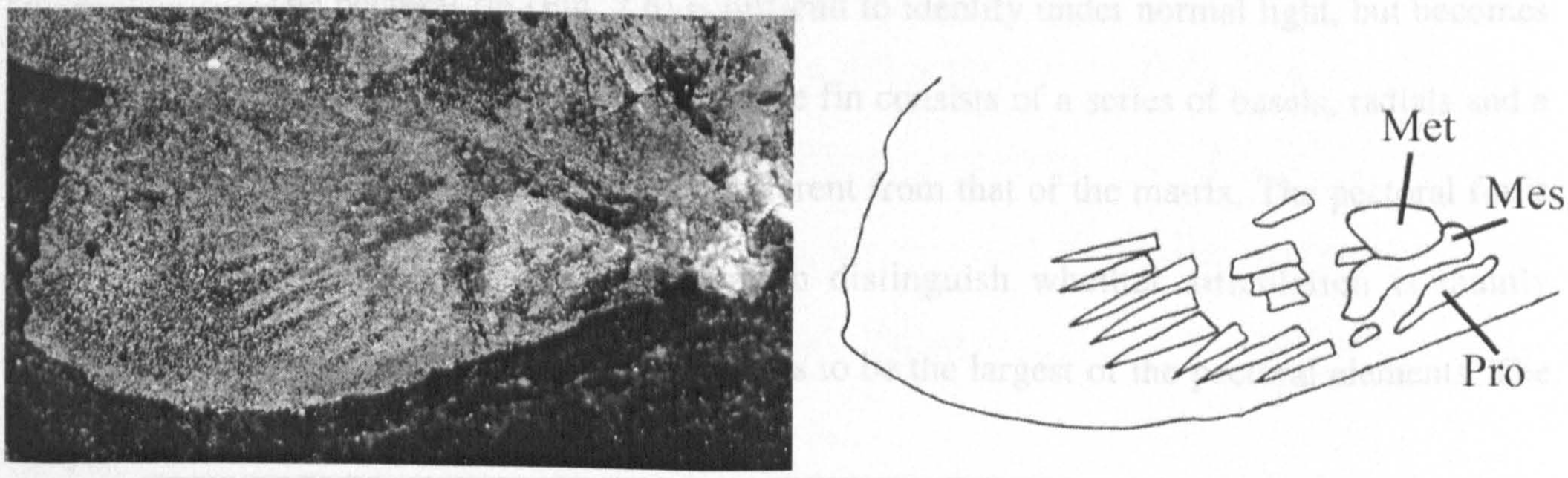


Fig. 2.6. *Polyacrodus twitchetti*. (V-2006-2). Pectoral fin. Tribasal with mainly propterygial articulation. Propterygium, mesopterygium and metapterygium have 1, 2-3, and 3-4 articulated radials rexpectively. Pro = propterygium, Mes = mesopterygium, Met = metapterygium.

The posterior fin spine is inserted at an angle of 77° and, like the anterior spine, almost meets the neural elements of the notochord. The posterior spine also has a triangular basal cartilage. There is evidence of four or five radials extending from the basal cartilage, though the preservation is inadequate to make out their structure. The internal structure of the posterior spine is similar to that of the anterior spine and again shows evidence of lesions acquired in life.

2.1.3.1.5 Scapulocoracoid

The specimen has a long and slender scapulacoracoid (Fig. 2.5 from counterpart) which extends from just below the anterior fin spine to the pectoral fin. Due to the compression and slight shearing, both scapulacoracoid processes can be seen. The scapulocoracoid arches posteriorly and possesses a medial line with two flanking grooves. Preservation of the structure is insufficient to distinguish between the scapula and coracoid regions, or to locate the glenoid fossa or diazonal foramen.

2.1.3.1.6 Pectoral fin

The pectoral fin (Fig. 2.6) is difficult to identify under normal light, but becomes clearer when viewed under UV light. The fin consists of a series of basals, radials and a fin web distinguishable by a colour different from that of the matrix. The pectoral fin is tribasal. Preservation is insufficient to distinguish whether articulation is mainly propterygial. The mesopterygium appears to be the largest of the pectoral elements. The

propterygium has one radial, the mesopterygium has two to three radials and the metapterygium has at least three to four, but it is likely that other radials were lost during preservation. When viewed under U.V. light there is a thin line in the upper area of the mesopterygium. This could be the proximal end of a radial sandwiched between the mesopterygium and the popterygium. The propterygial radial appears to be unjointed. While unclear, it appears that some of the mesopterygial radials have at least one joint. The structure of the metapterygial radials is too unclear to interpret. All distal radials taper to a point.

2.1.3.1.7 Pelvic girdle

Though the pelvic fin is missing, parts of the pelvic girdle are preserved. The girdle is preserved in lateral view with one half preserved above the other due to the compression and slight shearing of the fossil. This suggests that the girdle was in two halves and not fused. The base of the pelvic bar is quite pointed and faces anteriorly. A brown recrystallization covers the lower section of the girdle, masking detail, but one or possibly two radials can still be distinguished emanating from it.

2.1.3.1.8 Teeth

There are a number of teeth visible within the specimen, the clearest of which is an anteriorly positioned one. This tooth (Fig. 2.7) measures 1.10 mm and is preserved in lingual view, though which is uncertain. As well as this, another anterior tooth was originally found, but both were subsequently damaged. The principal cusp of the teeth is

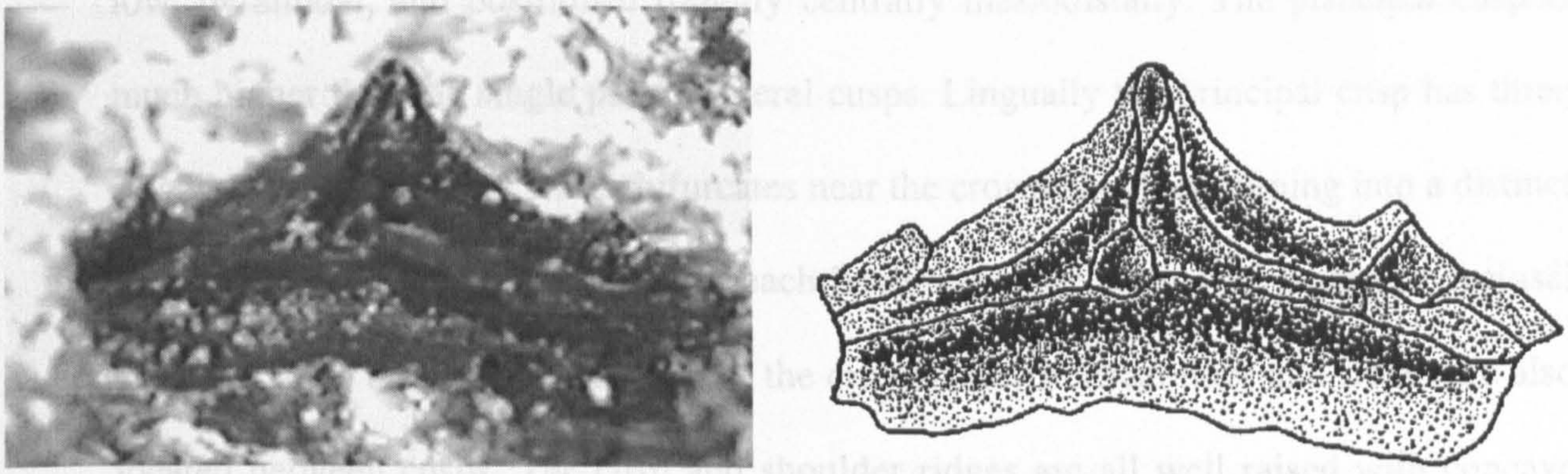


Fig. 2.7. *Polyacrodus twitchetti*. (V-2006-2). Partial anterior tooth taken under light microscope and illustration before it was broken.

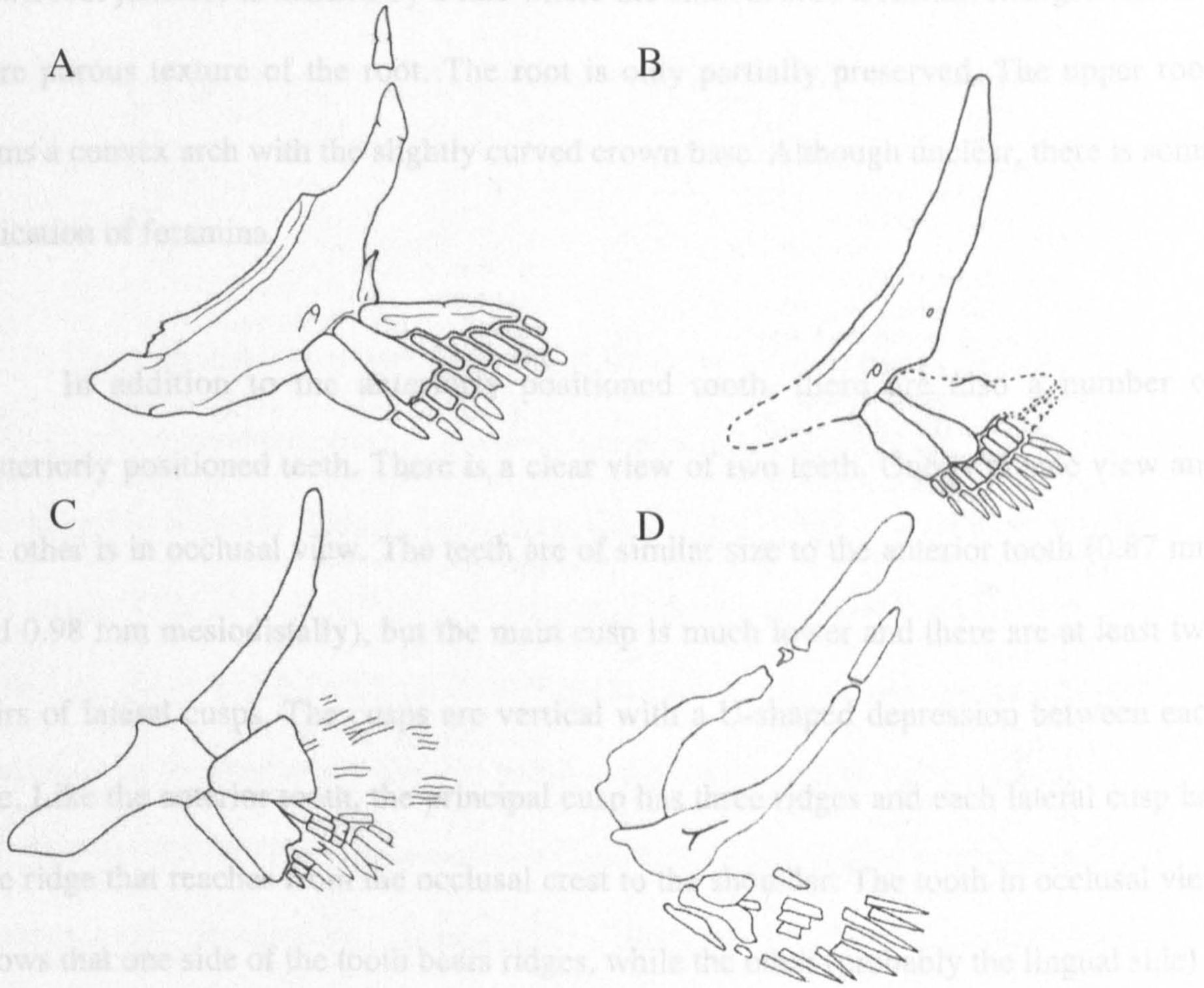


Fig 2.8. Pectoral fins of: A) *Lissodus cassagnesis*, B) *Hybodus hauffianus*, C) *H. fraasi*, D) *Polyacrodus twitchetti* (redrawn from Maisey 1982)

low, pyramidal, and positioned roughly centrally mesiodistally. The principal cusp is much higher than the single pair of lateral cusps. Lingually the principal cusp has three ridges, the central one of which bifurcates near the crown shoulder, turning into a distinct lingual projection. The lateral cusps each have one ridge extending from the occlusal crest that joins the peak of a node near the crown base. Vertical lines and ridges are also located between cusps. The cusp and shoulder ridges are all well raised with concave hollows between them. Below the shoulder, on the lingual side, the crown curves inwards towards the root, forming an overhang. There is no evidence of a labial projection. The crown root juncture is marked by a line where the smooth crown texture changes into the more porous texture of the root. The root is only partially preserved. The upper root forms a convex arch with the slightly curved crown base. Although unclear, there is some indication of foramina.

In addition to the anteriorly positioned tooth, there are also a number of posteriorly positioned teeth. There is a clear view of two teeth. One is in side view and the other is in occlusal view. The teeth are of similar size to the anterior tooth (0.87 mm and 0.98 mm mesiodistally), but the main cusp is much lower and there are at least two pairs of lateral cusps. The cusps are vertical with a U-shaped depression between each one. Like the anterior tooth, the principal cusp has three ridges and each lateral cusp has one ridge that reaches from the occlusal crest to the shoulder. The tooth in occlusal view shows that one side of the tooth bears ridges, while the other (probably the lingual side) is largely unornamented, but does possess a lingual peg. This tooth shows no indication of the labial peg. The tooth in side view also has an overhang from crown to root indicating

a labial view and again lacks the peg. The roots on the posteriorly positioned teeth are also poorly preserved, but, unlike the anterior tooth, the root top is a concave arch.

2.1.3.1.9 Dermal denticles

There is a high abundance of dermal denticle bases on the specimen, all of which are of a similar size indicating that the view is from interior of the specimen. The bases are fairly small (± 0.2 mm) and many have a square structure. The regular pattern of the denticles is similar to that of the recrystallization visible on the specimen but the two can be distinguished by the presence of a foramen in the center of the denticle bases.

2.1.3.1.10 Discussion

The teeth in this specimen differ from *Hybodus* and *Acrodus* in that they have a relatively squat pyramidal crown. However the question of whether the specimen should be assigned to *Lissodus* Brough, 1935, *Lonchidion* Estes, 1964, or a genus within the Polyacrodontidae is more complex. At present, *Lissodus* is known from full body fossils, while *Lonchidion* and the polyacrodontids are known only from isolated teeth. Several workers have commented on possible relationships of the genera based on tooth morphology. Duffin (1985) proposed that *Lissodus* and *Lonchidion* were synonymous, a contention later accepted by Cappetta (1987). However, the grouping of these two genera was based on several criteria later criticized by Antunes *et al.* (1990) because not all of the similarities are confined to the genera in question. Rees and Underwood (2002) later separated *Lissodus* and *Lonchidion* and placed them both in the family Lonchidiidae

along with *Hylaeobatis* and two new genera (*Vectiselachos* and *Parvodus*). *Polyacrodus* and *Lissodus* have always been considered separate genera but distinctions based on tooth morphology are not straightforward (Antunes *et al.*, 1990). There has been some debate over the diagnosis of *Polyacrodus* (Antunes *et al.*, 1990), as many of the early descriptions and illustrations are ambiguous (Johnson, 1981). In this work the characteristics of *Polyacrodus* are considered to be as given in the detailed review in chapter 3.1 (i.e. Anterior teeth with pyramidal shaped crown; Main cusp is centrally located and flanked by 1-4 pairs of prominent lateral cusps, cusps are symmetrical in distribution; Ornamentation consists of dense and fine to sparse and coarse ridges originating from the cusps and terminating at the crown/root junction, ridges do bifurcate; Posterior teeth are lower and wider than anteriors; main cusp is centrally located with 1-4 pairs of lateral cusps that are much less prominent than in anterior teeth; symmetry of cusps may vary by one on either side of main cusp; Ornamentation consists of dense and fine to sparse and coarse ridges originating from the cusps and terminating at the crown/root junction, ridges do bifurcate; Root of equal or greater depth than crown; Specialised foramina absent; Labial peg poorly defined or absent; Lingual peg absent; Longitudinal crest absent) and as such the specimen is assigned to the genus.

As this is the first specimen of *Polyacrodus* based on more than isolated teeth, a comparison of its morphology with that of other hybodonts is required to determine possible relationships. The cranium, branchial arches and pelvic girdle in the specimen are too badly damaged to allow comparison. The only structures that are complete enough to allow comparison are the teeth, the scapulocoracoid, the pectoral fin and the dorsal fin spines.

As stated earlier, the study specimen has a long and narrow scapulocoracoid. The structure of scapulocoracoids in hybodonts ranges from narrow bars seen in *P. twitchetti* and other sharks like *Lissodus africanus* (Brough, 1935) and *Hybodus fraasi* (Brown, 1900) to having massive coracoidal processes, as seen in *Lissodus cassangensis* (Antunes et. al., 1990). The results of an examination of the structure of scapulocoracoids are given in Table 2.1. No measurements are included from *L. africanus* due to the ambiguity of the original illustration and lack of measurements (Brough, 1935). Broom (1909) did provide dimensions for the scapulocoracoid in *L. africanus,* though the upper portion of the scapula and lower portion of the coracoid were missing, preventing accurate comparison. The definition of a thin scapulocoracoid is taken to be a ratio of less than 0.2 in the proportion width / length. Width is defined as the maximum limits of the coracoid and length as the maximum distance between the extreme ends of the scapula and coracoid.

It can be seen from Table 2.1 that all of the Carboniferous and many of the Triassic hybodonts possess thin scapulocoracoids, while only the Triassic hybodont *Lissodus cassangensis* possess a broad scapulocoracoid. It is possible that the reconstruction of *L. cassangensis* is inaccurate due to one scapulacoracoid being superimposed on the other. From this, it can be taken that thin scapulocoracoids are primitive, and hence the slender structure of the scapulocoracoid in *P. twitchetti* does not imply a relationship between *Polyacrodus* and any hybodont family.

Species	Length of scapulacoracoid/ maximum width
Onychoselache	0.184
Tristychius arcuatus	0.173
Hamiltonichthys mapesi	0.150
Wodnika striatula	0.255
Hybodus fraasi	0.160
Hybodus hauffianus	0.182
Lissodus cassangensis	0.257
Study specimen	0.140

Table 2.2. Ratio of length : maximum width of scapulacoracoid; *Onychoselache* (Woodward 1924), *Trystychius arcuatus* (Dick 1978), *Hamiltonichthys mapesi* (Maisey 1989), *Wodnika striatula* (Schaumberg 1977), *Hybodus fraasi* (Brown 1900), *Hybodus hauffianus* (Koken 1907), *Lissodus cassangensis* (Antunes *et al.* 1990)

The Mesozoic hybodont genera *Hybodus*, *Lissodus* and *Hamiltonichthys* (Maisey, 1989) are all represented by specimens with preserved pectoral fins. *Hybodus hauffianus* has a large pro- and mesopterygium with the metapterygium being the largest pectoral element. This is also seen in *H. fraasi* and *L. cassangensis. P. twitchetti*, however, has a relatively small propterygium and the mesopterygium is the largest pectoral element, a character which is unusual for hybodonts. In *H. hauffianus* the pro- and mesopterygium both support three radials. The number of radials on the metapterygium in unclear. This arrangement differs from that seen in *L. cassangensis* which has a propterygium supporting one radial, mesopterygium supporting three and the metapterygium supporting five. The configuration found in *L. cassangensis* is consistent with what is seen in *P. twitchetti*, though it has only three to four metapterygial radials (others could be missing). The first metapterygial radial in *L. cassangensis* is sandwiched between the meso- and metapteryium. This is also seen in *P. twitchetti* and in *Hamiltonichthys.* Though the pectoral fin in the study specimen shows some similarities to both *Hamiltonichthys* and

Lissodus, these similarities are not sufficient to imply a close relationship between these genera and *Polyacrodus.*

Dorsal fin spines in various hybodont genera are distinguishable by their lateral ornamentation and the pattern of the posterior denticles (Maisey, 1978). Both of these are too poorly preserved in *P. twitchetti* to allow comparison. In *L. africanus* the posterior fin spine is shorter than the anterior one, while in *L. cassangensis* it is the contrary, as is the case in *P. twitchetti. P. twitchetti* has a triangular basal element at the base of each spine, with only the posterior spine possessing a full complement of calcified radials, a feature seen in all hybodonts. The anterior fin spine in *L. africanus* lies at an angle of 45°, while the posterior spine lies at an angle of 70°. The anterior and posterior spines of *L. cassangensis* lie at angles of 27° and 64° respectively. *P. twitchetti's* anterior and posterior fin spines lie at angles of 48° and 74° (similar to those of *L. africanus*). This is, however, no proof of relatedness, because similar angles have been found in species of *Hybodus* (Von Urlichs *et al.,* 1979) in addition to which the spines could have changed angle post mortem.

As can be seen from the above comparisons there is little evidence that would support any close relationship between *Polyacrodus* and any other hybodont family.

2.1.3.2 *Lissodus angulatus*

Cohort Euselachii Hay, 1902

Superfamily Hybodontoidea Owen, 1846

Family Lonchiididae Herman, 1977

Genus *Lissodus* Brough, 1935

Lissodus angulatus (Stensiö, 1921)

1921 *Polyacrodus angulatus* Stensiö: 31, fig. 13, pl. 1 fig 27.

1979 *Polyacrodus angulatus* Jerzmańska: 25, figs. 14-17.

1985 *Lissodus angulatus* Duffin: 119, figs. 11a-c.

1989 *Lissodus angulatus* Duffin: 84, fig. 1c.

1992 *Lissodus angulatus* Gomez Pallerola: fig. 9c.

1993 *Lissodus angulatus* Duffin: fig 6c.

2001 *Lissodus angulatus* Duffin: fig.. 11a-c.

Revised diagnosis: Teeth measuring up to 7 mm in length, with moderate central main cusp; lateral cusps absent, but may show incipient development; labial peg moderate. Crown has single ridge descending on main cusp, bifurcating basally into longitudinal ridge along labial crown shoulder. Where known, root is subequal in length to crown and there is an obvious overhang between them. Specialised foramina present along the upper labial root face. All other foramina irregular, but may be organised into longitudinal rows on both lower labial and lower lingual root faces. All teeth long and symmetrical. Lateral teeth relatively narrow with prominent labial peg. Jaw deep and robust with pronounced posterior process.

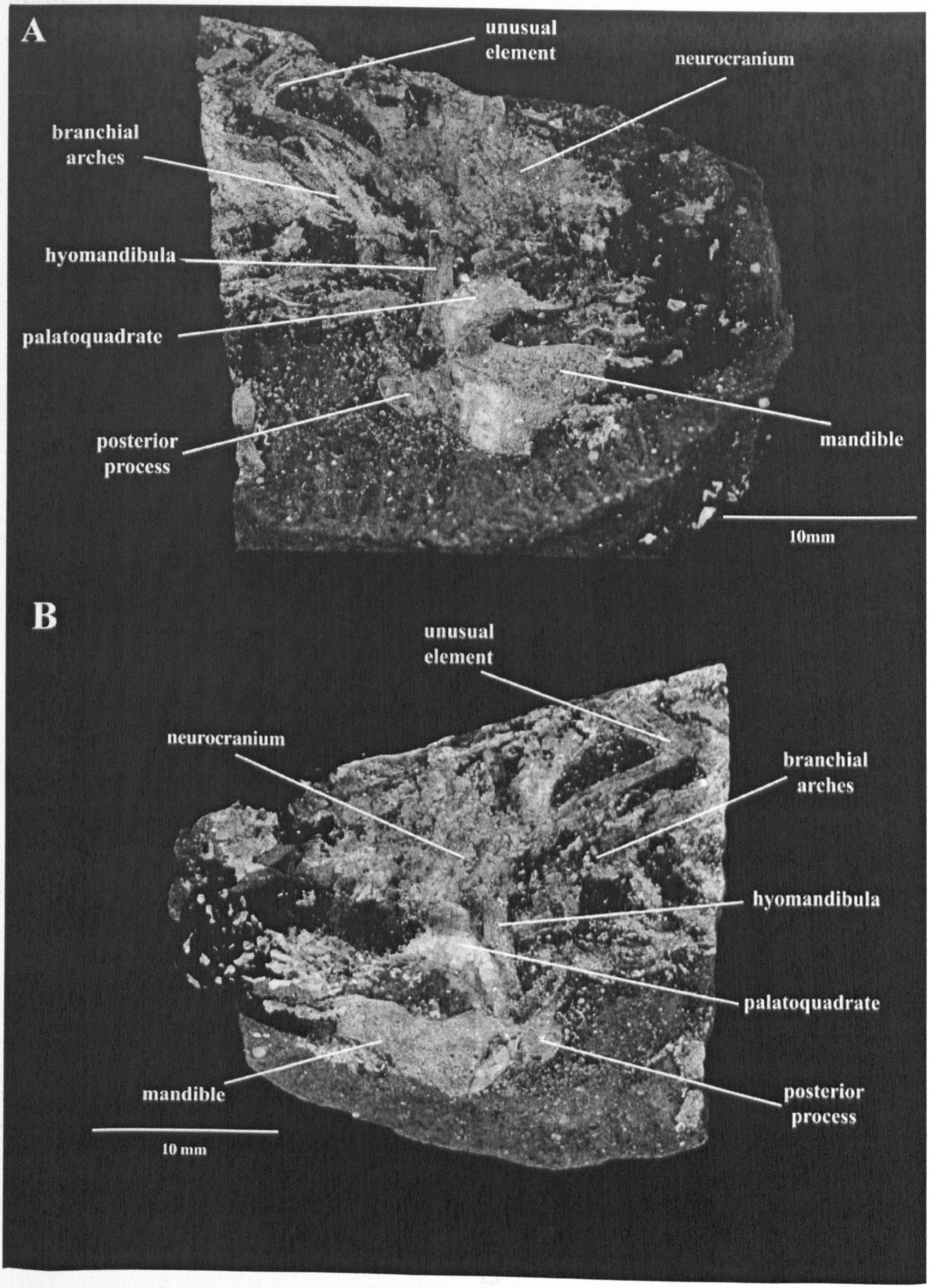


Fig. 2.9. Head section of *Lissodus angulatus* (V-2006-1), A. part, B. counterpart

Type locality: Fish Horizon 1 (*Posidonomya* bed) *Otoceras/Ophiceras* zone (Induan), Spitzbergen

Type specimen: Reported by Stensiö to be in the collection of Salomon at Heidelberg.

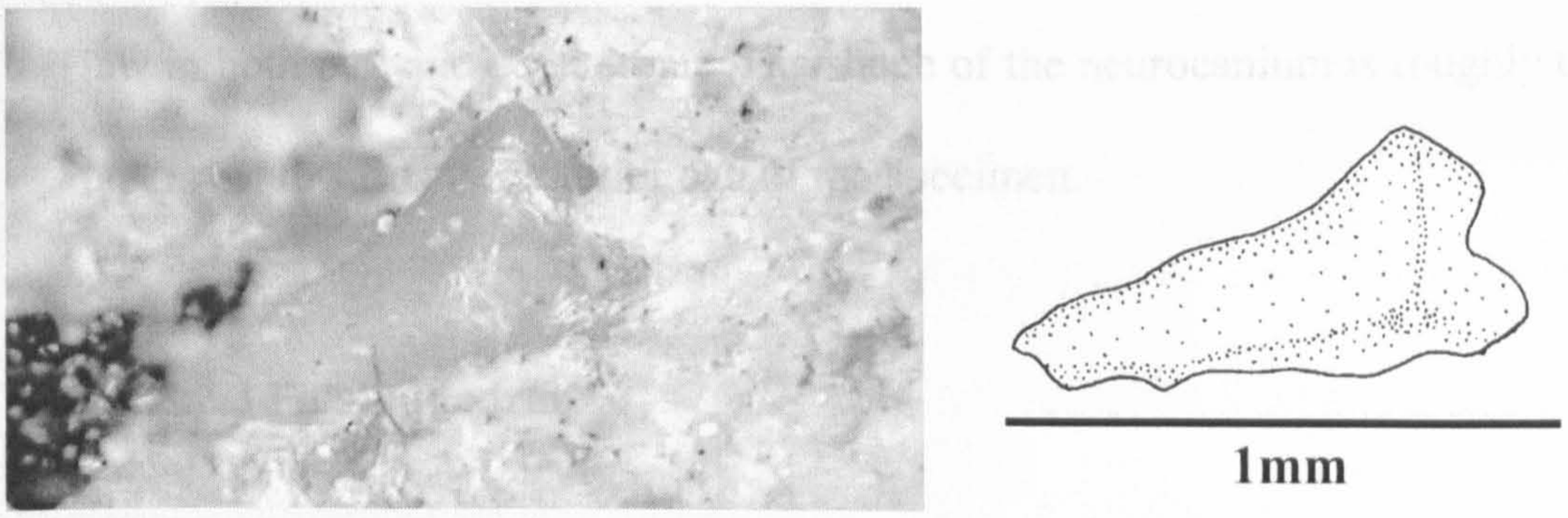
Specimen no: V-2006-1a/b

2.1.3.2.1 Teeth

The teeth visible in the specimen are broad, squat and pyramidal, and they lack roots (Fig. 2.10). Though the teeth are encased in the matrix (and hence each can only be viewed from one angle) several different teeth are preserved in various orientations. They display a moderately elevated central cusp, but do not possess any lateral cusps. The teeth are small (maximum length 1.97 mm mesio-distally) and approximately three times as long as high. A vertical striation descends from the central cusp labially and bifurcates basally. The labial side possesses a moderate peg. The remainder of the labial side is smooth and unornamented. The teeth are arranged in rows but preservation is insufficient to attempt a reconstruction of the dental apparatus.

2.1.3.2.2 Neurocranium

The neurocranium is visible as a vague area of compressed cartilage fragments but has been severely damaged and it is impossible to identify much detail of the remains. The preserved length of the neurocranium is 13.6 mm, roughly equal to that of the lower



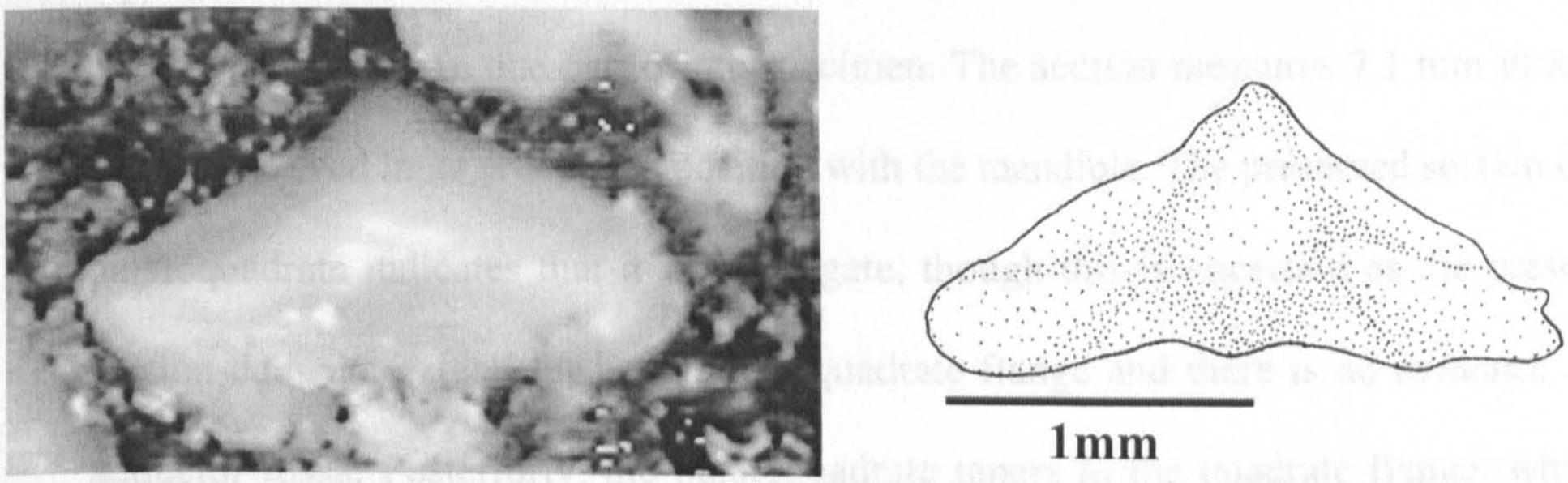
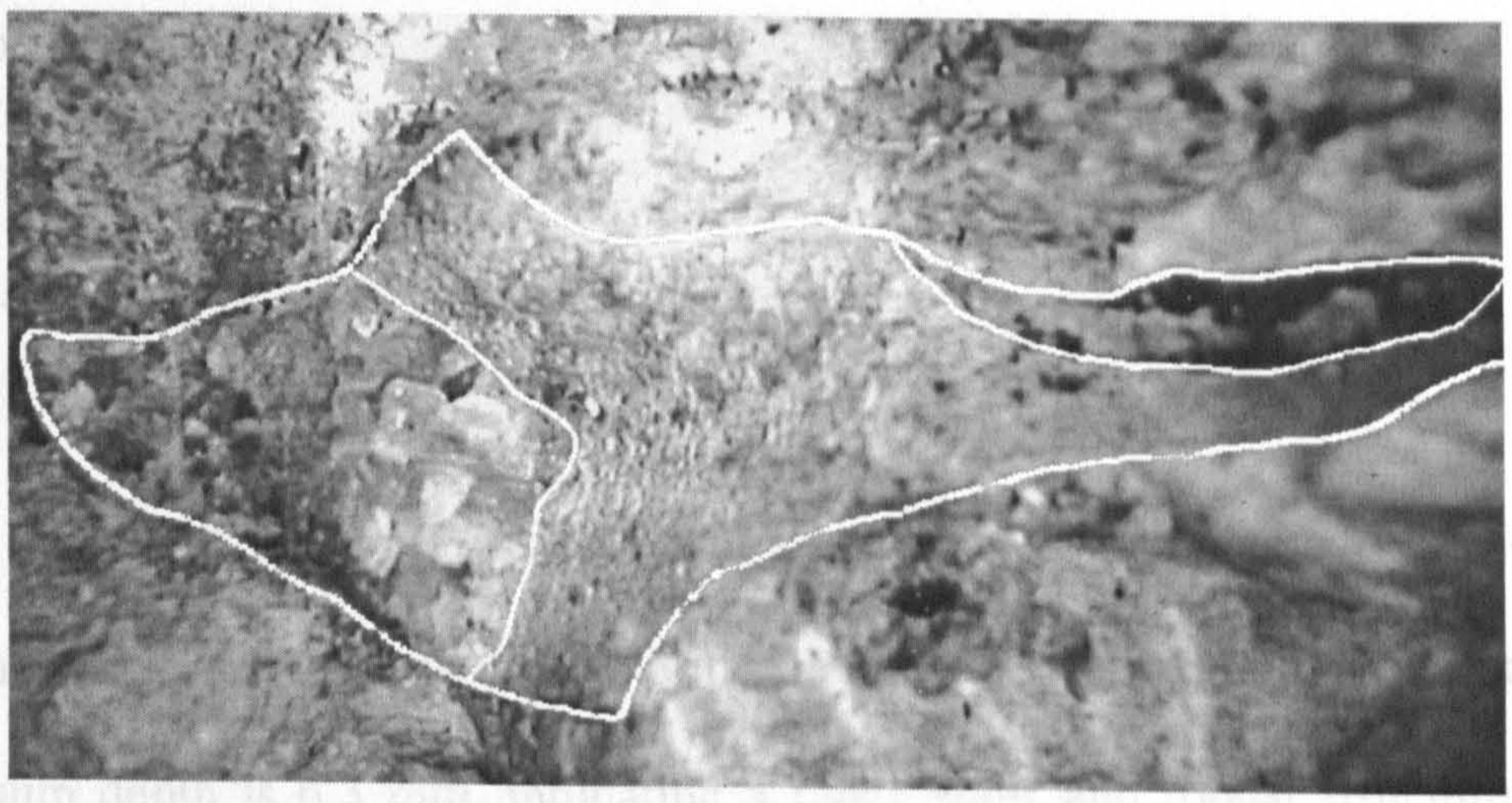


Fig. 2.10. Teeth of *Lissodus angulatus*. (V-2006-1). A, photograph and illustration of a tooth in labial view B, photograph and illustration of a tooth in lingual view.



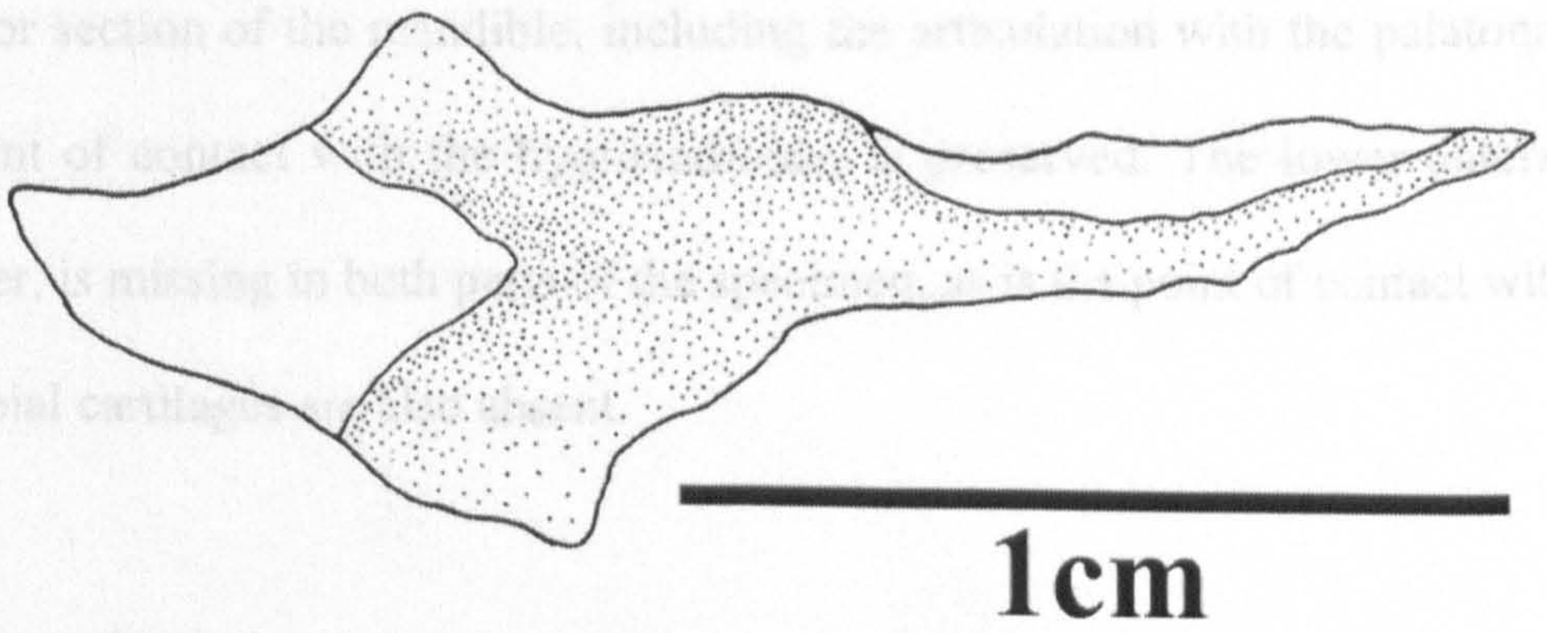


Fig. 2.11. Enhanced view of mandible of *Lissodus angulatus* (V-2006-1). A, photograph with white line delineating extremities; B, outline sketch.

jaw in both part and counterpart. The shape of the neurocanium is roughly triangular that tapers off towards the anterior end of the specimen.

2.1.3.2.3 Palatoquadrate

A small area of the right palatoquadrate, roughly one third of its original length, has been preserved in one part of the specimen. The section measures 7.1 mm in length and is preserved in its articulated position with the mandible. The preserved section of the palatoquadrate indicates that it was elongate, though this is uncertain as the preserved section does not extend far beyond the quadrate flange and there is no evidence of an adductor fossa. Posteriorly, the palatoquadrate tapers to the quadrate flange, which is narrow in comparison to other hybodonts especially at its point of contact with the mandible (Maisey 1982).

2.1.3.2.4 Mandible

The right mandible (Fig.2.11) is by far the largest preserved structure in the specimen. Its preserved length is 18.3 mm in one part, 19 mm in the counterpart and the maximum depth is 6.3 mm, indicating a fairly short and robust structure. The entire posterior section of the mandible, including the articulation with the palatoquadrate and the point of contact with the hyomandibula, is preserved. The lower anterior section, however, is missing in both parts of the specimen, as is the point of contact with the teeth. The labial cartilages are also absent.

At the posterior end, the mandible seems to thin down into a large dorsally extending projection, which is broken off from the main portion of the mandible. It is possible that this is the ceratohyal, which has been compressed under the mandible, but the continuous nature of the extension makes this unlikely.

The aforementioned process is damaged and it is impossible to distinguish its three-dimensional structure. Virtually all of the remaining preserved jaw fragment is preserved in three dimensions, though only visible in lateral view. The anterodorsal region of the jaw is elevated relative to the rest of the mandible and there is a marked convexity towards the depressed anteroventral region. The point of contact of the mandible with the palatoquadrate is also depressed, with the joint concealed beneath the palatoquadrate. Finally, there is a marked elevation from the center of the mandible towards the posterior section until the three-dimensional structure ceases to be preserved just before the beginning of the posterior process.

2.1.3.2.5 Hyomandibula

The hyomandibula is visible as a stout bar that emerges from the preserved section of the neurocranium. It extends behind and past the preserved section of the palatoquadrate, but stops short of the point of contact of the palatoquadrate with the mandible. The preserved section is 6.0 mm long and has a maximum thickness of 1.6 mm at the lowest point, closest to the jaw joint.

2.1.3.2.6 Branchial skeleton

The specimen contains various elements of the branchial arches. These have been crushed and several elements are missing, preventing the description of the arrangement of the elements, but some can still be identified. There are at least two identifiable epibranchials, which are visible as bars that are preserved reclining anteriorly at an angle of 15° to the horizontal (long axis of the body), and are approximately 7.4 mm in length, beginning 2.6 mm behind the centre point of the preserved section of the hyomandibula. At least one pharyngobranchial is visible, reclining posteriorly at an angle of 49° to the horizontal, which is approximately 6.5 mm long and is located directly above the first epibranchial. A lightly coloured area immediately behind the visible pharyngobranchial may contain further pharyngobranchials, which have been crushed. The arrangement of the first pharyngo- and epibranchial is similar to that seen in *Hybodus fraasi* (Maisey 1982).

Directly above the visible pharyngobranchial is an unidentified skeletal element, which may or may not be part of the branchial skeleton. The element is a thin elongate bar, which reclines posteriorly at an angle of 25° to the horizontal, and extends posteriorly from the rear of the neurocranium. The preserved section of the bar is 7.0 mm long, but without being able to identify it, it is impossible to be sure whether or not it is complete. At the posterior end of the element, which is located above the damaged portion of the branchial arches, is an articulation with another element reclining anteriorly at an angle of 49°, which is approximately 4.5 mm long. This element curves and expands into a horn shape towards the anterior end of the specimen. It is possible that

this thin bar is an epibranchial and that the horn-shaped structure with which it articulates is a pharyngobranchial. If this is the case, it would mean that the epibranchial and pharyngobranchial were displaced upward and rotated 180° while remaining articulated and all other branchial elements were disarticulated or destroyed while remaining in approximate relative positions.

2.1.3.2.7 Discussion

The current specimen is assigned to *Lissodus angulatus*. The teeth are identical to those identified by Stensiö (1921) and Jermañska (1979) as *Polyacrodus angulatus* and later reassigned to *Lissodus angulatus* (Duffin 1985). Historically *Lissodus* is a poorly defined genus. Duffin (1985) proposed the following diagnostic criteria for *Lissodus*, which were later extended by Antunes *et al.* (1990): "low principal cusp expanded into a broad labial peg, not supported by any development of the root, greater depth of the labial face, incised crown/root junction at the tooth extremities, deeply undercut lower lingual surface of the tooth crown, and shallow lower labial surface, triangular shape of root attachment area, concentrated labially, presence of a longitudinal pulp cavity, overlap of teeth in adjacent files and presence of lingual pressure scars". These definitions are, however, vague and overlap with several other genera, such as *Lonchidion* and *Polyacrodus*.

Rees & Underwood (2002) distinguish between *Lissodus* and *Lonchidion*, though both are put in the family Lonchidiidae. One of the most obvious characters separating

the teeth of *Lissodus* and *Lonchidion* is a well developed crown shoulder in the latter, particularly obvious on the lingual side.

Previously the Early Triassic distribution of *Lissodus angulatus* was thought to have been restricted to the Olenekian of Spitzbergen but this latest find also places it in the Induan of Greenland, increasing both its geographic and stratigraphic range.

The "unusual process" at the posterior part of the mandible in the current specimen merits further discussion. This is unusual in hybodonts and is not displayed in any of the Mesozoic hybodonts described by Maisey (1982), but it is not unique. Dick (1978) described another hybodont, *Tristychius arcuatus*, from the Carboniferous of Scotland; that also displayed a process, though less pronounced, on the posterior end of the mandible. The mandible in this case was, however, much narrower. While never reported in other *Lissodus* species, presence of a similar process in other hybodonts means cannot be autapomorphic in the *Lissodus angulatus*. It is possible that the process is a pathological deformation, though this seems unlikely. It is also possible that the process is an adaptation to the animal's diet though exactly how is unclear. The jaw in extant sharks is closed using the quadratomandibularis muscle that stretches between the palatoquadrate and the anterior area of the mandible (i.e. in front of the jaw joint). The posterior process, therefore, could not be used to create a more powerful bite. Suggesting any more detailed functional morphological purpose for the process without further evidence or material would be purely speculative.

2.2 The fossil shark fauna of the Lower Triassic of Madagascar

2.2.1 Introduction

The present study specimens were collected from the Lower Triassic beds of Madagascar. One (Specimen A) was given to the author by Gilles Cuny who in turn had received it from Francois Escuillé. The others are located in the Milan Museum of Natural History, Italy. The main Lower Triassic fossil fish localities in Madagascar occur in outcrops in the northern and western region of the island. The geographical and geological background of Madagascar is outlined in Beltan (1996). In brief, the sedimentary beds range from the Carboniferous to the Jurassic and can be divided into three groups, the second of which (the Sakamena Group) contains the fish beds. These fish-bearing beds within the Middle Sakamena Group correspond to the Olenekian, Lower Triassic when a warm and shallow, epicontinental sea, with a depth of 200-300m covered the area (Beltan 1996).

The fish beds from Madagascar have been studied since the beginning of this century. As well as the abundant fish fossils, the Lower Triassic palaeocommunity of Madagascar contained temnospondyls (Lehman, 1961), basal anurans (Rage and Rochek, 1989), basal anapsids (Lehman, 1966) as well as plants and invertebrates (Collingnon, 1933, 1934; Besairie 1972). Merle (1908) gave the first description of actinopterygians and Woodward (1910) the first study of coelacanthids. These papers were the first in a long line of literature to study the ichthyology of this region. The fossil imprints that come from this area are often very detailed and allowed the precise description of the

anatomy of many Lower Triassic ichthyofaunas. Thus far, thirty-six species of Actinopterygii and Sarcopterygii have been described from the Lower Triassic of Madagascar (Beltan, 1996) but as yet there has been only one shark description from the area (Thomson, 1982). Sharks have also been described from other Lower Triassic African sites, most notably *Lissodus africanus* the type species of *Lissodus* from the Karoo of South Africa (Broom, 1909).

2.2.2 Material and Methods

The specimens are preserved as part and counterpart in nodules. In all cases there is no preserved skeletal material. The skeletal elements have been preserved as impressions that, when prepared and filled with silicon rubber, produce positive peels. The first is partially preserved with the skull, branchial arches, scapulacoracoids, both pectoral fins, first dorsal fin spine, ribs and vertebral column present but the posterior portion of the body including the second dorsal, anal and caudal fins missing. The second is also only partially preserved. The anterior section is present, including a nearly complete meckel's cartilage and palatoquadrate, scapulacoracoid, and anterior fin spine. The neurocranium, branchial arches and pectoral fins however are not preserved. The third fossil is composed of the posterior section of the neurocranium, the dorsal column and the anterior fin spine. There is another section of dorsal column and a second fin spine preserved within the same nodule. This could be the disarticulated rear section of the same animal or it could be from a different shark. The final specimen is composed of a pair of pelvic fins fin. The first three fossils are of comparable size and the first two

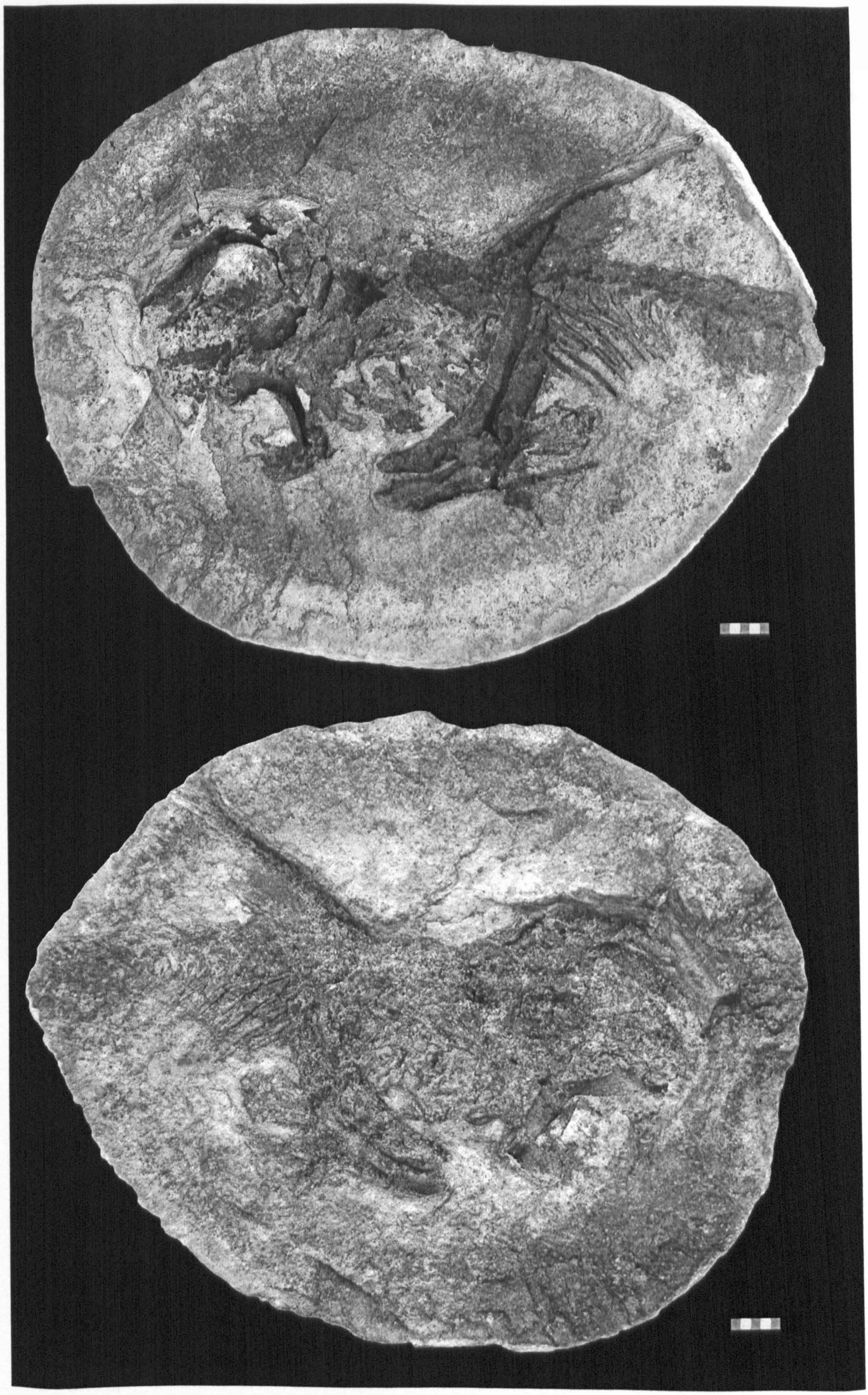


Fig 2.12. A, part and B, counterpart of *Lissodus* sp. A (RHM D2-85). preserved in a nodule.

display teeth with the same general morphology. The fourth fossil is clearly from a much larger shark.

2.2.3 Systematic Palaeontology

2.2.3.1 *Lissodus* aff. *cassangensis*

Cohort Euselachii Hay, 1902

Superfamily Hybodontoidea Owen, 1846

Family Lonchidiidae Herman, 1977

Genus *Lissodus* Brough, 1935

Lissodus aff *cassangensis* Texeira, 1956

(Fig. 2.12)

2.2.3.1.1 Specimen (sp. no RHM D2-85)

Note: Only one side of the nodule was moulded in silicon rubber as the other side was too delicate.

2.2.3.1.1.1 Neurocranium

The skull (Fig. 2.13) has been crushed laterally destroying much of the detail in the neurocranium. Despite the compression there is still a vague outline of the neurocranium with a few recognisable structures. The upper surface of the neurocranium inclines steeply from the top of the supraorbital crest to the tip of the snout. The orbit is

recognisable in positive relief. Behind is a vague shape, which is likely to be the post orbital process. The anterior portion of the skull is visible and there are several indistinct structures, which could be the lateral optic process or the occipital cotylus, but the skull has been too badly crushed to make a positive identification of these structures. Most of the lower section of the neurocranium has also been too badly damaged to identify.

2.2.3.1.1.2 Palatoquadrate

Both halves of the palatoquadrate are preserved in mesial view. One bar shows far better preservation than the other with the anterior portion being almost perfect. The posterior section is less well preserved. It is possible to make out the anterior section of the quadrate flange but the posterior section is obscured. The palatoquadrate is slightly ventrally displaced.

This palatoquadrate (Fig. 2.14) is elongate, 14 mm maximum length, 3.5 mm maximum depth. The anterior third of the structure is composed of a stout bar with a pronounced downward slope from the palatine process towards the tip. The palatoquadrate has a pronounced downwards slope anteriorly from the palatine process until the beginning of the quadrate flange when it once again extends into a bar. The most prominent features are the pronounced ethmoid articulation towards the anterior end, the palatine process and the (incompletely preserved) quadrate flange. The ethmoid articulation is visible as a concave surface oriented upwards and forwards at the anterior part of the palatoquadrate. This surface obviously articulated with an ethmoid process though no evidence of this structure remains. The palatine process is visible as an extension at the highest point of the structure. And marks the thickest point on the

palatoquadrate, which slopes towards both the anterior and posterior ends. Only the anterior section of the palatine process is preserved. This slopes down at an angle of roughly 25° to the horizontal from a point halfway along both the length and height of the palatoquadrate. This then levels out at a point slightly lower than the anterior section to form the beginning of the quadrate flange. The posterior section of the quadrate flange is missing.

2.2.3.1.1.3 Meckel's cartilage

Both halves of the Meckel's cartilage have only been partially preserved in the specimen. In one half, the posterior portion is visible extending from the posterior of the palatoquadrate. The point of contact between the palatoquadrate and the Meckels cartilage (the jaw joint) is obscured beneath the palatoquadrate. It then extends ventrally at an angle of 138° to the palatoquadrate (an angle not possible in life) suggesting that the jaw was dislocated *post mortem*. Roughly half of the structure (7 mm) is preserved in this orientation. A further 6 mm is preserved, extending ventrally from the tip of the posterior section at an angle of 90°. The extreme anterior section of the Meckel's cartilage is missing. The total preserved length is 13 mm. The second half has been displaced dorsally, above the palatoquadrate towards the neurocranium. This half has also been broken with the anterior section located slightly anteriorly and ventrally of the posterior section. The overall preserved length is 15.5 mm and the maximum depth is 3.5 mm. It is relatively deep compared to those of other hybodonts such as *Hybodus*. There is a marked concavity in the postero-dorsal section just before the jaw joint.

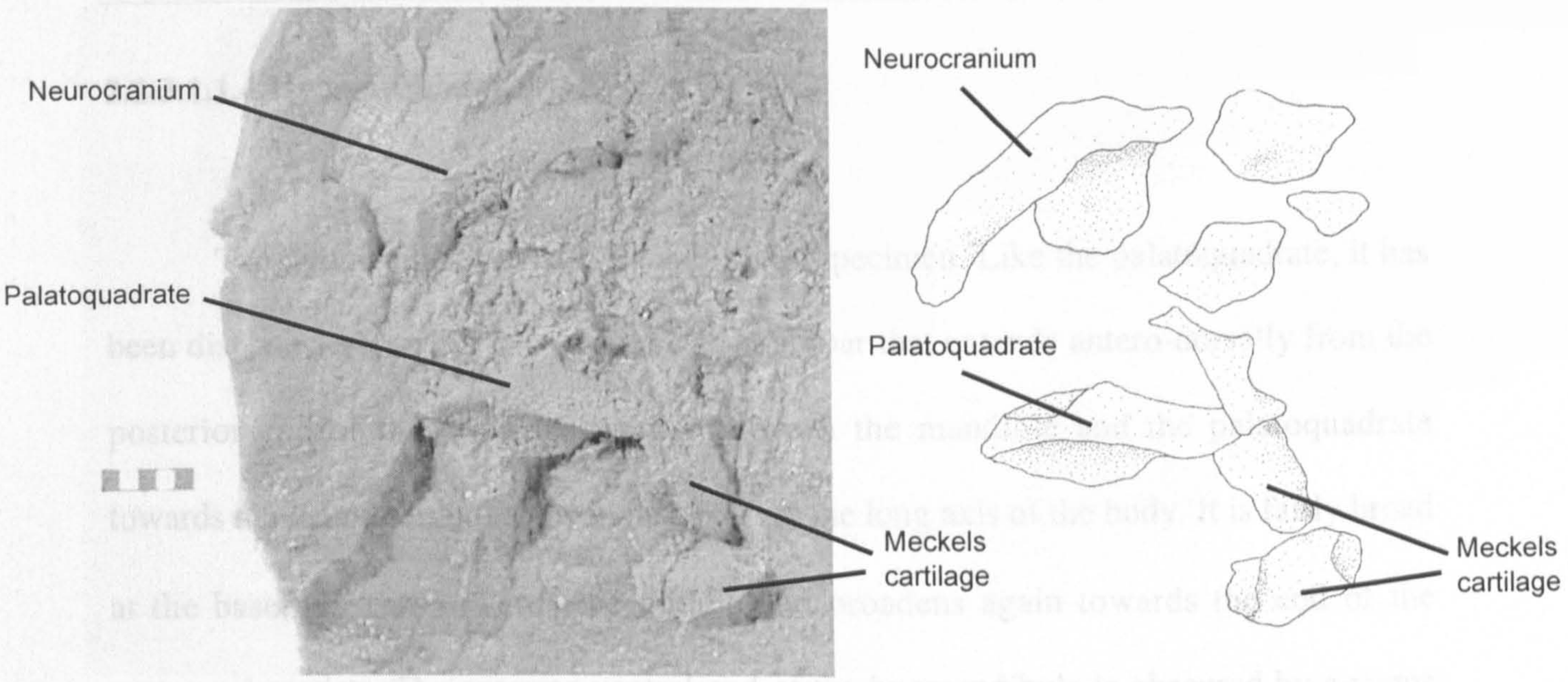


Fig. 2.13. skull of *Lissodus* sp. A (RHM D2-85)

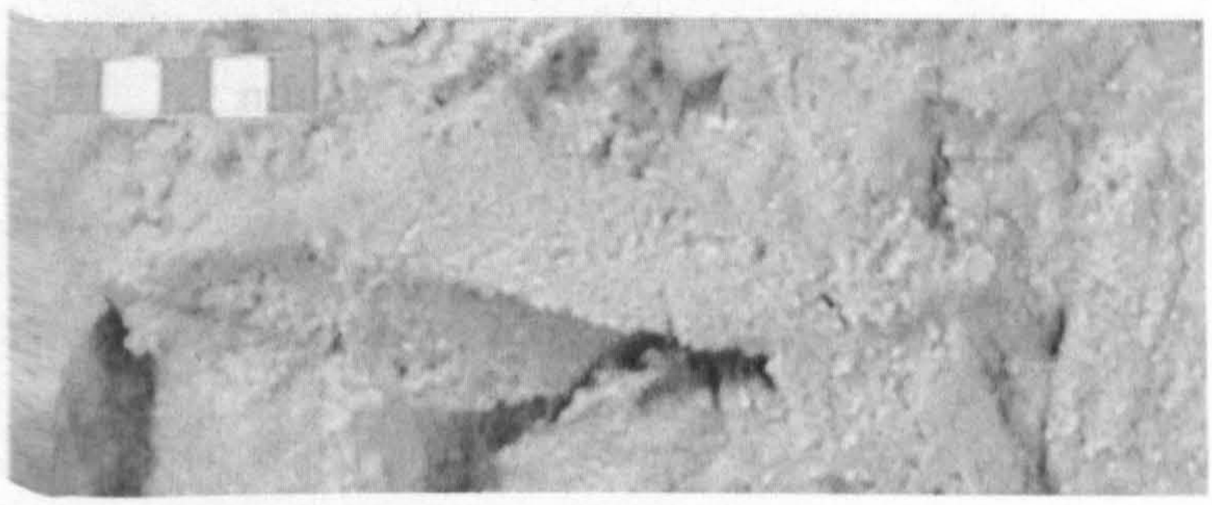


Fig. 2.14. palatoquadrate of *Lissodus sp*. A (RHM D2-85)

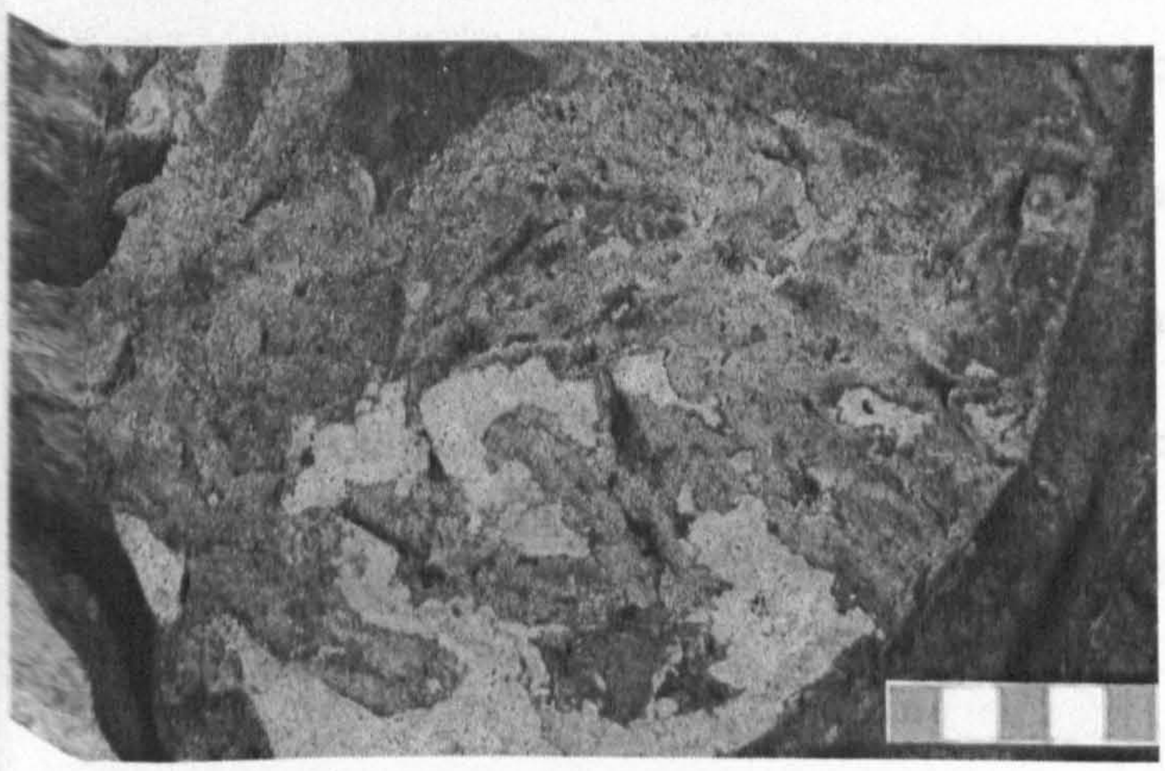


Fig. 2.15 Branchial arches of *Lissodus sp*. A (RHM D2-85)

2.2.3.1.1.4 Hyomandibula

The hyomandibula is also visible in the specimen. Like the palatoquadrate, it has been displaced ventrally. It is visible as a stout bar that extends antero-dorsally from the posterior end of the point of contact between the mandible and the palatoquadrate towards the neurocranium at an angle of 68° to the long axis of the body. It is fairly broad at the base, narrows towards the middle and broadens again towards the end of the preserved section. The extreme ventral end of the hyomandibula is obscured by a vague structure, possibly a very poorly preserved section of the postorbital process. The preserved length of the hyomandibula is 7 mm; it is 3 mm and 2.5 mm thick at the extreme ventral and dorsal ends respectively and 1.5 mm at its thinnest point in the middle section.

2.2.3.1.1.5 Branchial skeleton

The branchial arches are indistinct on the peel and so are figured from the original specimen (Fig. 2.15). The branchial elements have been crushed, obscuring most of the detail. Compression of the structures means that the two sides of the branchial skeleton have been superimposed making it difficult to discern the number and orientation of the branchial elements. There are four visible (posteriorly reclining) pharyngobranchials as well as six (anteriorly reclining) epibranchials, though from which side they originate is unclear. No ceratobranchials, hypobranchials or basibranchials are visible. The structure is vaguely similar to that of *Lissodus cassangensis*, though the lack of lower branchial

elements make comparison difficult. Based on the available evidence there seem to have been five gills.

2.2.3.1.1.6 Vertebral column

Though only partial, the vertebral column is well preserved and can be seen in reasonable detail. From the posterior tip of the neurocranium to the end of the preserved section, the vertebral column measures 50 mm. Four or five, ventrally displaced, interdorsal elements are visible between the posterior extremity of the neurocranium and the anterior dorsal fin spine. The displaced scapulacoracoid immediately below the fin spine is likely to be concealing several elements. There are eight visible, posteriorly reclining interdorsal elements originating from beyond the area obscured by the scapulacoracoid and terminating at the end of the preserved section of the specimen (27 mm). Three of the four anterior-most of the interdorsal elements originating posteriorly from the scapulacoracoid have anteriorly reclining basiventral elements associated with them. These basiventral elements then extend into ribs. One the counterpart there are at least six other ribs positioned posteriorly to the four ribs originating from the basiventrals. It is, however, unclear whether these additional ribs are all from one or both side of the animal.

2.2.3.1.1.7 Dorsal fin

Only the anterior dorsal fin is present in the specimen. The fin has both the imprint of the spine and the fin webbing (visible as dermal denticles) preserved. The triangular basal cartilage is barely visible as it is obscured beneath the imprint of the fin webbing. The spine is inserted at an angle of 38° to the horizontal, is 26.5 mm in length and at its deepest point meets the vertebral column. A detailed imprint of the outer ornamentation of the spine is preserved within the matrix and five smooth longitudinal ribs are clearly visible.

2.2.3.1.1.8 Scapulacoracoid

The scapulacoracoid (Fig. 2.16) in the specimen has been dorsally displaced and extends from beyond the ventral tip of the anterior fin spine to below the branchial arches. From tip to tip, the structure is 25 mm long. Due to the compression and slight shearing, both halves can be seen. Preservation of the scapulacoracoid is fairly good and it is possible to distinguish between the scapular and coracoid regions at the point of contact with the pectoral fin. Preservation is not good enough to locate finer detail such as the glenoid fossa or diazonal foramen.

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THE SPINE

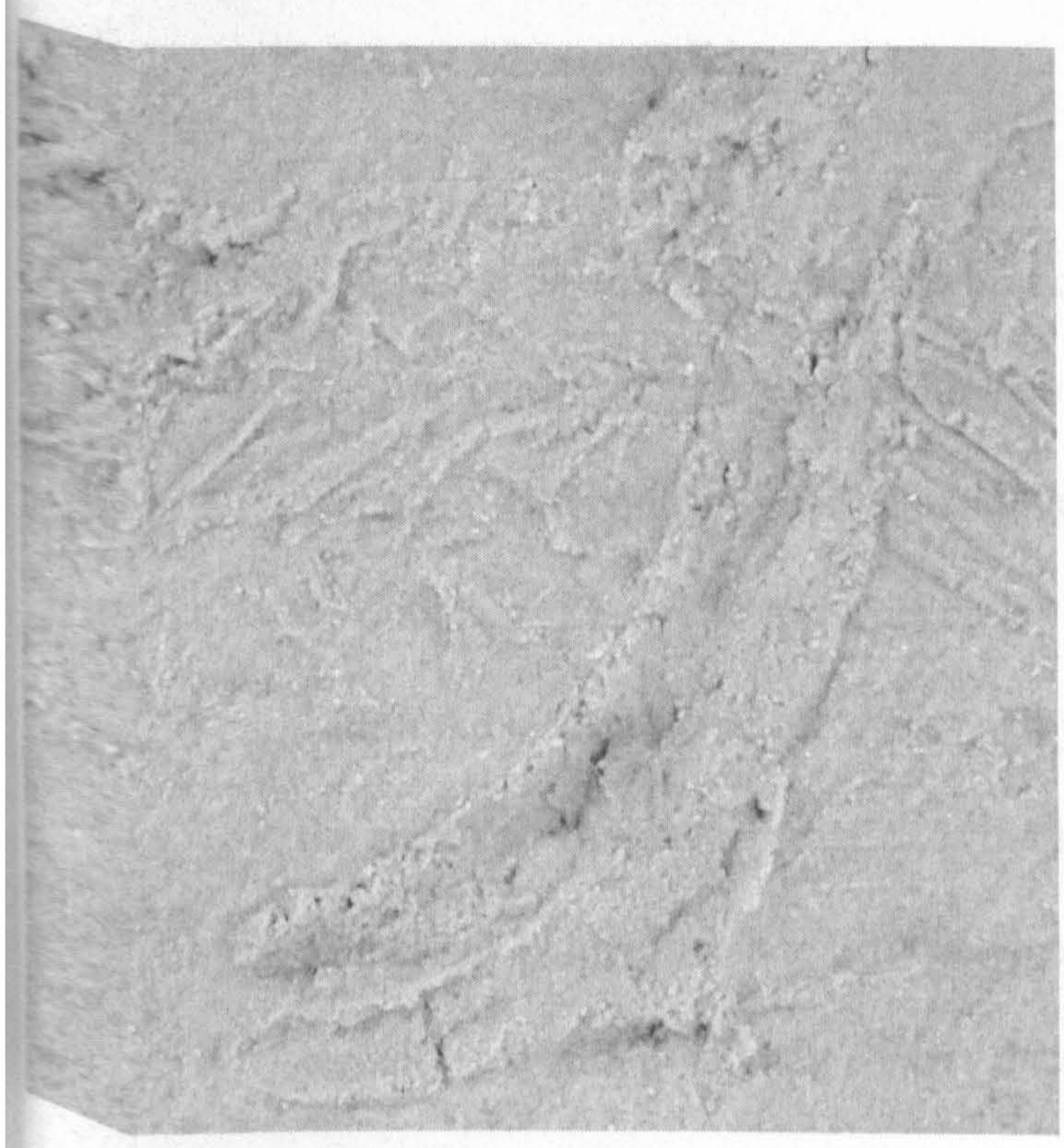


Fig. 2.16. Scapulacoracoid of *Lissodus* sp. A (RHM D2-85)

Fig. 2.17. Pectoral fin of *Lissodus* sp. A (RHM D2-85)

2.2.3.1.1.9 Pectoral fins

The pectoral fins, like the branchial arches are far more distinct on the original specimen than on the peel. Both pectoral fins (Fig. 2.17) are preserved within the specimen with enough detail to make out the basal elements though there is no evidence of radials or fin webbing. The meta- and mesopterygial elements are well preserved within the left fin while the meso- and propterygial elements are better preserved within the right fin. The metapterygium is the longest basal element and has a roughly triangular shape and is tapering towards the mesopterygium. The mesopterygium is the thickest element and is only slightly shorter than the metapterygium. It has a thin point of contact with the scapulacoracoid (0.5 mm) gradually expanding to the radials (3 mm). The propterygium is the smallest element and it has a roughly similar sized contact with the scapulacoracoid as the metapterygium. The propterygium gradually curves round to meet the metapterygium just short of its posterior extremity.

2.2.3.1.1.10 Teeth

There are a few tooth impressions (Figs. 2.18 A and B) contained in the fossil. The preservation of these imprints is good enough to get an outline of the tooth shape and some of the ornamentation, though a complete picture is difficult to reconstruct. The teeth are preserved in labial and occlusal views. Superficially, the teeth are short and pyramidal with a peg visible on the labial side.

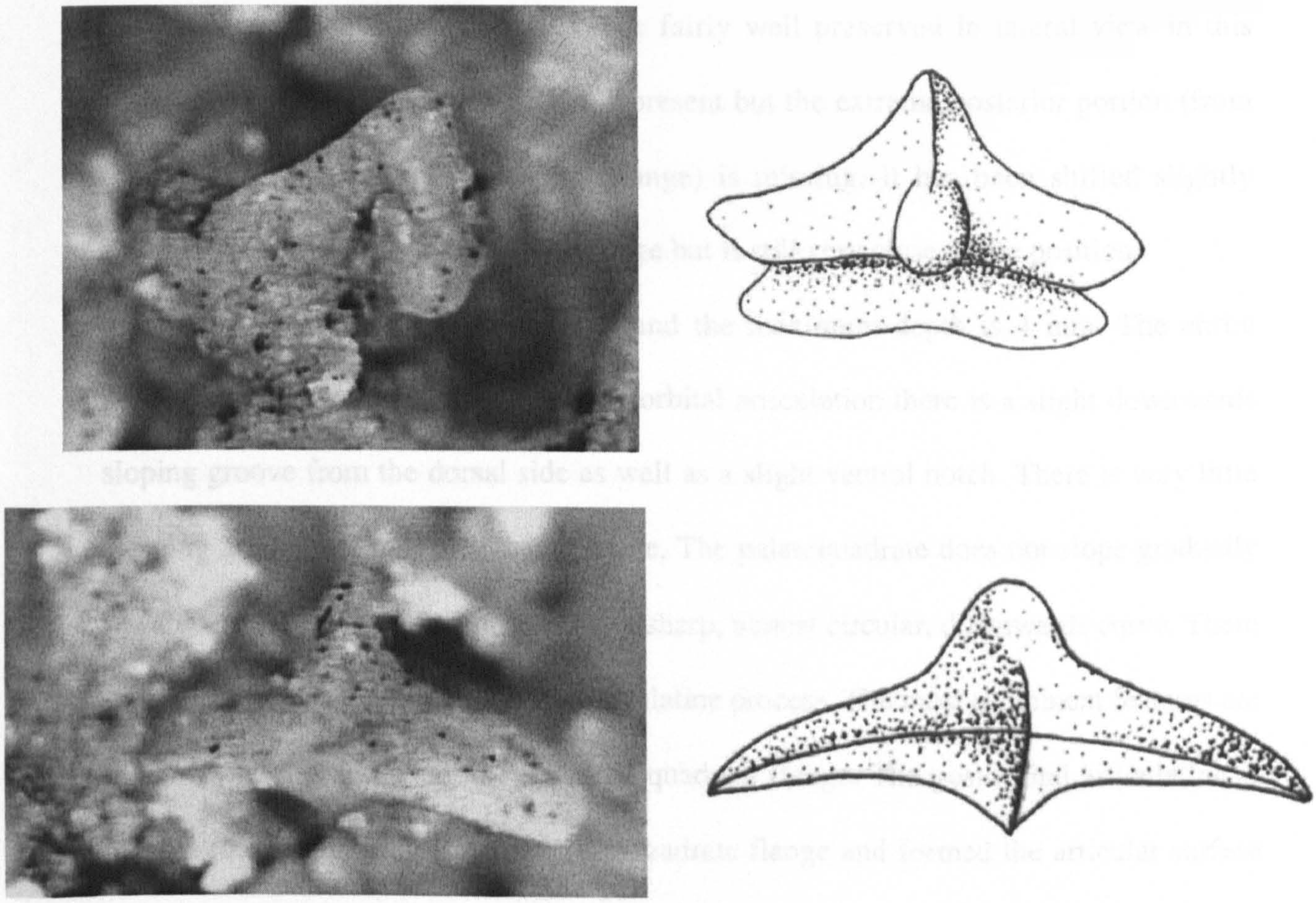


Fig. 2.18. Labial and occlusal views of *Lissodus* sp. A teeth. A, preserved length 0.85mm. B, preserved length 1.2mm (RHM D2-85)

2.2.3.1.2 Specimen B (sp. no V-2006-3)

2.2.3.1.2.1 Palatoquadrate

The palatoquadrate (Fig. 2.19) is fairly well preserved in lateral view in this specimen. The entire anterior section is present but the extreme posterior portion (from roughly halfway along the quadrate flange) is missing. It has been shifted slightly anteriorly, relative to the Meckel's cartilage but is still very close to life position.

The overall length is 15.5 mm and the maximum depth is 4 mm. The entire palatoquadrate is a stout bar. At the postorbital articulation there is a slight downwards sloping groove from the dorsal side as well as a slight ventral notch. There is very little thinning at any section along the structure. The palatoquadrate does not slope gradually towards the anterior end but instead has a sharp, almost circular, downwards curve. There is no sign of the ethmoid articulation or palatine process. The most prominent features are the postorbital articulation and the large quadrate flange. The postorbital articulation is located roughly half the way along the quadrate flange and formed the articular surface with the post orbital process on the neurocranium. This groove then slopes up to join the rest of the posterior section of the palatoquadrate with no obvious delineating ridges surrounding it. There is a postero-ventrally sloping ridge that begins roughly one third of the way along the palatoquadrate. This ridge continues ventrally forming an overhang, which turns into the quadrate flange roughly four fifths of the way along the palatoquadrate. While the posterior section of the quadrate flange was not preserved it can be reconstructed and would have extended ventrally to the lowest point of the

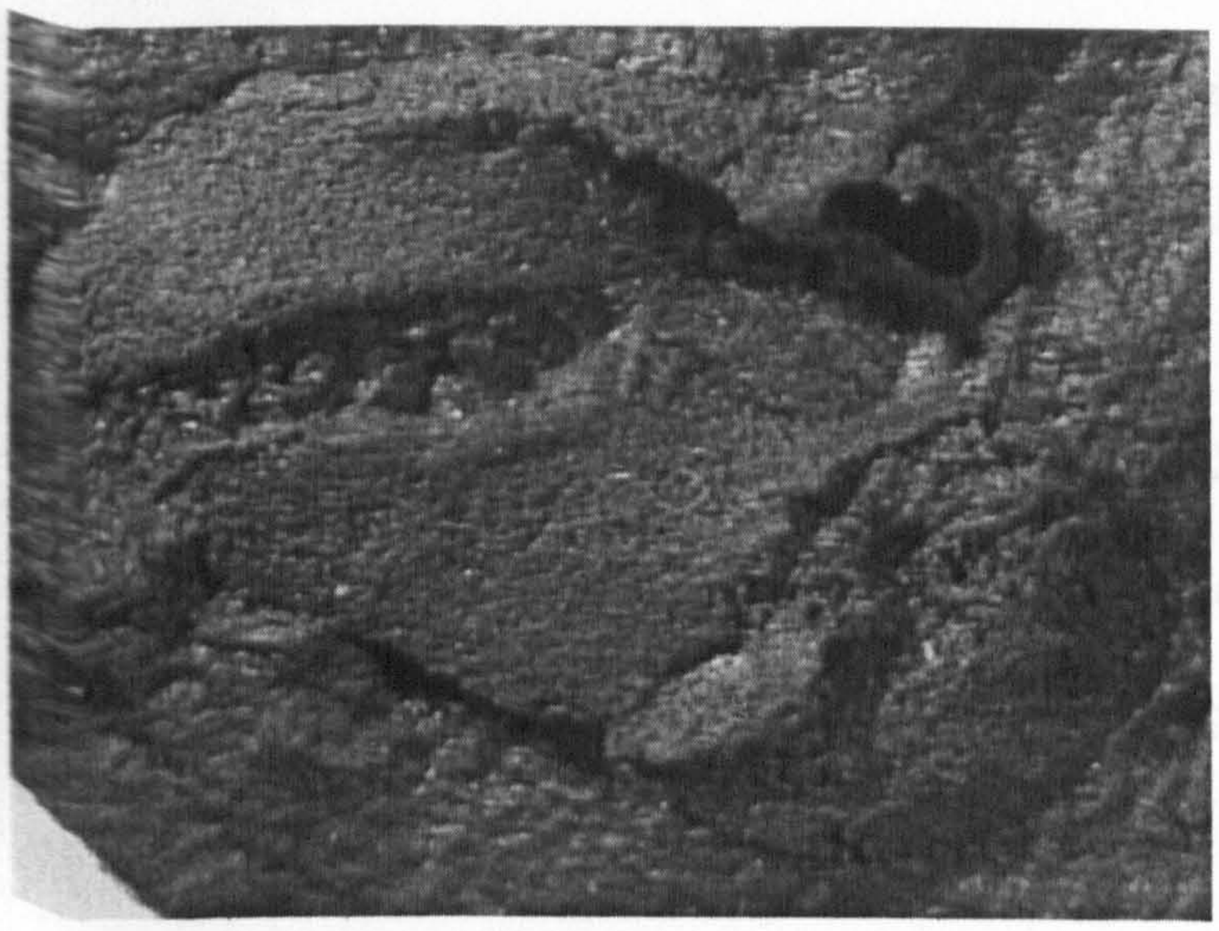
palatoquadrate covering the articulation between the palatoquadrate and the meckels cartilage (Fig. 2.19).

2.2.3.1.2.2 Meckel's cartilage

The Meckel's cartilage, like the palatoquadrate, has been preserved almost complete in lateral view. The extreme anterior section is missing and the posterior surface is obscured by matrix. In addition to this there is a break and a degree of scouring from the middle section to the posterior surface of the mandible distorting the view of the lateral surface. Relative to the palatoquadrate the Meckel's cartilag is located slightly more dorsally than it would have in life. The maximum length of the mandible is 16 mm with the maximum depth being 7.5 mm. From the anterior tip, the ventral margin slopes down steeply at an angle of 37° to the thickest point of the palatoquatrate. It then curves steeply to form the posterior surface. The anterior half of the Meckel's cartilage dorsal margin has a ridge that is possibly the site of attachment for the lower dental battery. The jaw joint is obscured by matrix and a portion of the palatoquadrate.

2.2.3.1.2.3 Vertebral column

The vertebral column in this specimen is very poorly preserved. From the posterior of the head to the end of the preserved section it measures 50.5 mm. There are no preserved interdorsal elements between the head region and anterior fin spine. Posterior to the anterior fin spine there are five visible posteriorly reclining interdorsals.



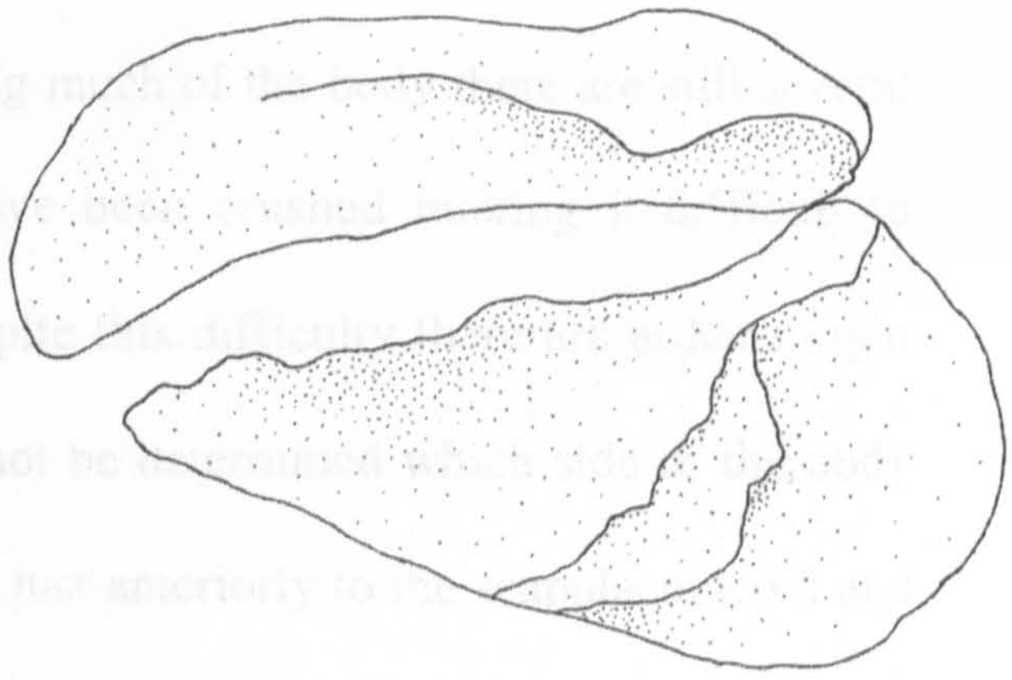


Fig. 2.19. Jaw apparatus of *Lissodus* sp. B (V-2006-3)

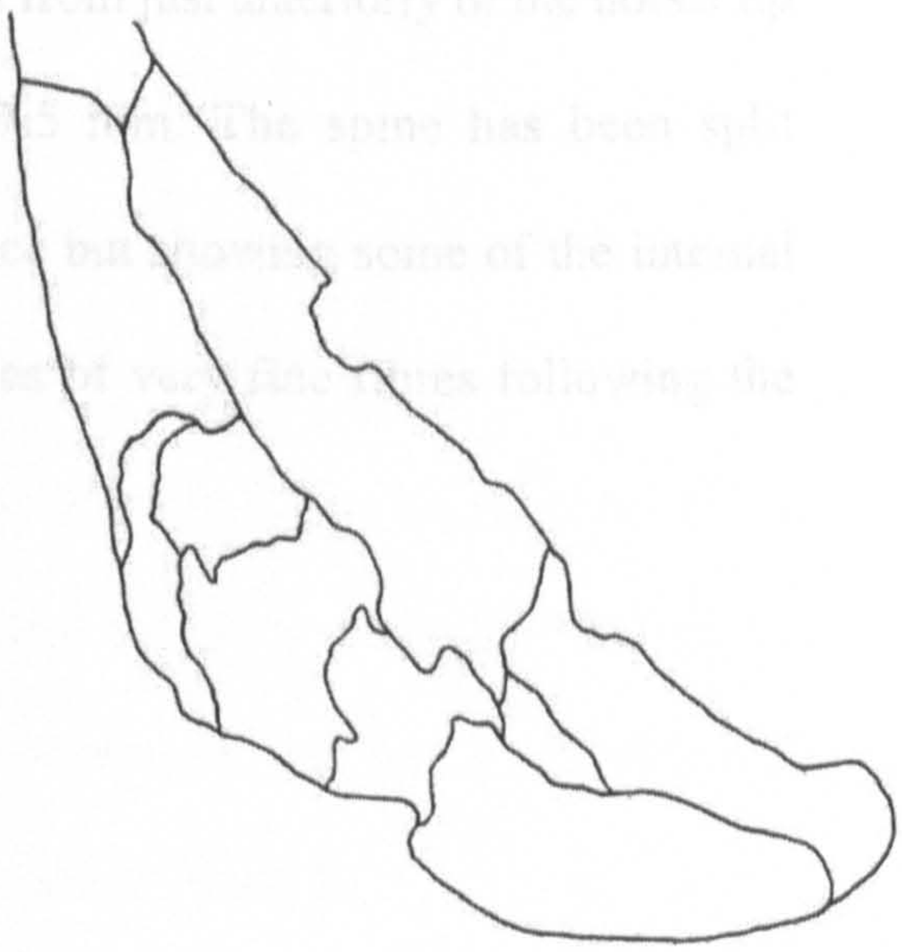


Fig. 2.20. Scapulacoracoid of *Lissodus* sp. B (V-2006-3)

These interdorsals, that would have been located just anterior to the posterior fin spine, have associated basiventral elements though these basiventrals do not extend into ribs. Though there are no interdorsal elements along much of the body there are still several visible ribs in the specimen. These ribs have been crushed making it difficult to distinguish between individual elements. Despite this difficulty there are at least eight visible anteriorly reclining ribs though it cannot be determined which side of the body they originate from. This tangle of ribs begins just anteriorly to the scapulacoracoid and extends for 24 mm behind it.

2.2.3.1.2.4 Dorsal fin

Only the anterior finspine is present in the specimen. Roughly two thirds of the anterior spine has been preserved with the distal third missing. There are no preserved posterior denticles on the finspine. The spine extends from just anteriorly of the dorsal tip of the scapulacoracoid at an angle of 44° for 17.5 mm. The spine has been split longitudinally masking any detail of the outer surface but showing some of the internal structure. The internal structure is visible as a series of very fine fibres following the length of the spine.

2.2.3.1.2.5 Scapulacoracoid

The two halves of the scapulacoracoid (Fig. 2.20) have been superimposed on top of each other. There are multiple fractures and a large amount of scouring obscuring almost all of

the detail from the surface of the scapulacoracoidal bars. The outline shape can however still be made out. From tip to tip, the scapulocoracoid is 30.5 mm long. Like the previous one this specimen has a long and slender scapulacoracoid. This specimen, however, has a much wider base than the previous fossil and is relatively thicker. There is a small section of cartilage extending from the ventral end of the scapulacoracoid may be part of the pectoral fin; however the structure has been very badly damaged and it is impossible to make out any detail.

2.2.3.1.2.6 Teeth

The teeth are only preserved in occlusal view. From this view they are virtually identical to the teeth of the specimen previously described in specimen A.

2.2.3.1.3 Specimen C ((sp. no V-2006-4)

This specimen consists of a partial neurocranium, partial vertebral column and two finspines. The neurocranium is seen from ventral view and is preserved from the posterior tip of the to just anteriorly of the postorbital process. The dorsal column has been broken and disarticulated with the posterior section being at roughly 52° to the anterior section. There are no preserved teeth within the specimen but due to its small size it is provisionally assumed to be the same as specimens A and B.

2.2.3.1.3.1 Neurocranium

The neurocranium (Fig. 2.21) is visible in ventral view. It is not preserved in three dimensions but only as a crushed imprint of the ventral side. The preserved section is 13.5 mm long and 14 mm wide. From the anterior end, the neurocranium curves out steeply into what would have been the postorbital processes. The extreme ends of the postorbital processes are missing, indicating that the neurocranium would have been wider in life. The remains of the postorbital process then curves round to form the occipital region and eventually recurves inwards to meet the occipital cotylus. There is a groove bisecting the neurocranium longitudinally. This could be where the floor of the uncalcified notochord area has collapsed.

Despite the relative lack of three-dimensional preservation there are still structures recognisable on the ventral surface of the neurocranium imprint. There are two grooves originating just anteriorly to the occipital cotylus, which extends in a curve, anteriorly and laterally. These grooves are most likely the grooves for the lateral dorsal aorta. These end in two pits that are the foramina for the orbital arteries. Just anteriorly to these foramina, and exactly on the medial line of the neurocranium is a pit for the internal carotid artery.

Fig. 2.21. Neurocranium of *Lissodus* sp. C (V-2006-4)

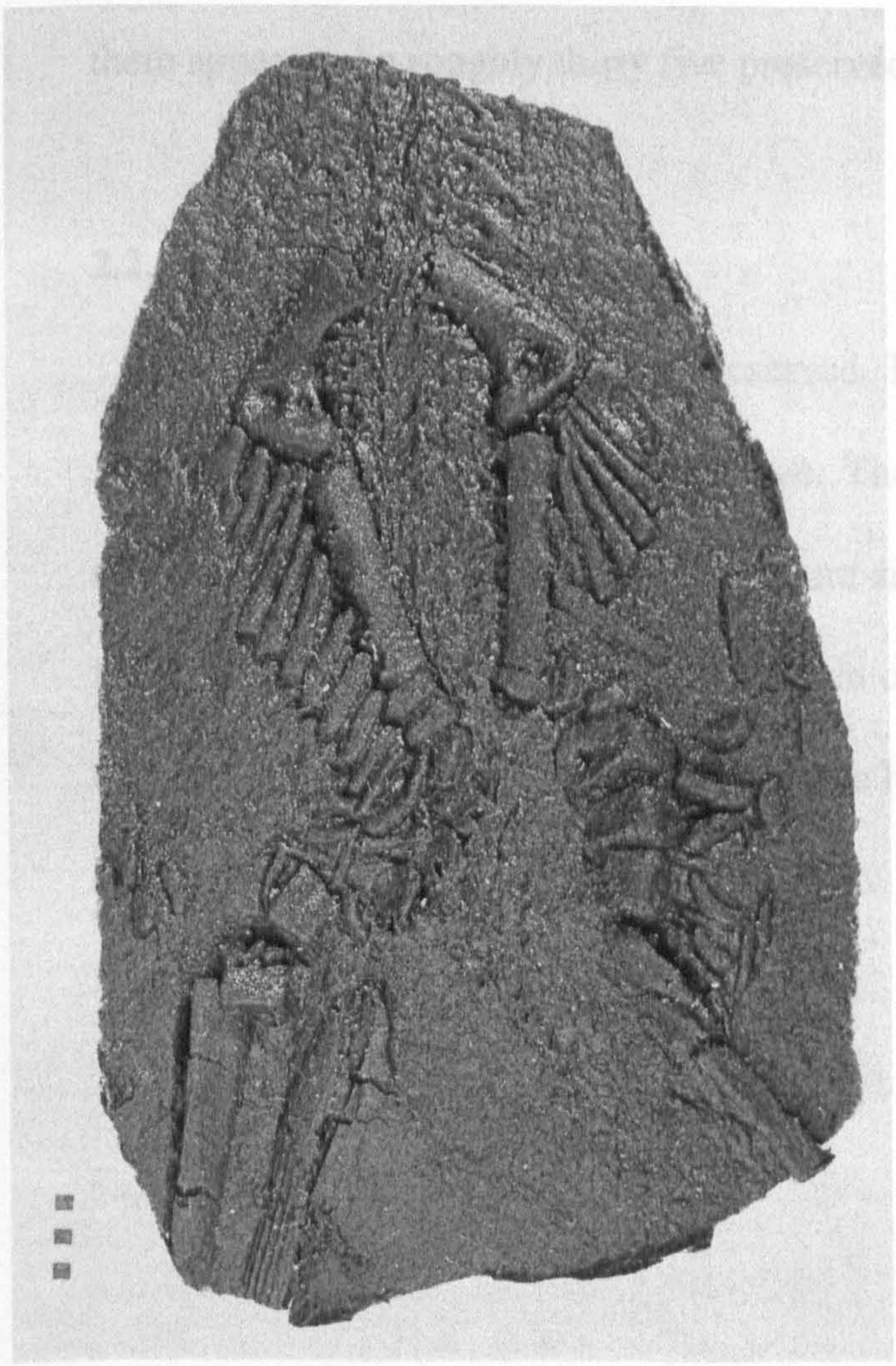


Fig. 2.22. pelvic fin of Hybodontoidea indet. (V-2006-5)

2.2.3.1.3.2 Branchial skeleton

All that remains of the branchial skeleton is four posteriorly reclining pharyngobranchials. All other elements from the branchial arches have been destroyed during fossilisation.

2.2.3.1.3.3 Vertebral column

The axial skeleton consists of the dorsal column made up entirely of interdorsal elements. There are no preserved basiventrals or ribs. Though it is difficult to make out, there appear to be roughly thirty five preserved interdorsals.

2.2.3.1.3.4 Dorsal fins

Both fin spines have been preserved. The first lies at an angle of 45°, is 24.5 mm long and has associated basal cartilage. The visible ornamentation on this specimen consists of four longitudinal ribs. There are six or seven preserved posterior denticles on the spine. The second spine lies at an angle of 53° is 35 mm long and has no associated cartilage. The outer surface of this fin spine has been damaged thus none of the external ornamentation has been preserved.

2.2.3.2 Hybodontoidea indet

Cohort Euselachii Hay, 1902

Superfamily Hybodontoidea Owen, 1846

Indet.

2.2.3.2.1 Specimen D (sp. no V-2006-5)

The current specimen consists of a pair of pelvic girdles, fins and the vertebral column running between them. There is no other material associated with the fossil that would allow the positive identification of this shark to generic level.

2.2.3.2.1.1 Pelvic girdle

The pelvic girdle (Fig. 2.22) is 55 mm long and 11 mm wide at its widest point. The anterior end of the girdle is very thin, then roughly half way along its length it widens out very quickly into a broad bulbous shape. There are two very clear diazonal foramina present on the pelvic girdle. The first three radials articulate with the pelvic girdle. Six radials articulate with the pelvic metapterygium and one further with each of the three basal segments of the metapterygium. Anteriorly to the three basal segments are five intermediate elements lacking radials and the mixipterygium. The terminal clasper complex that would have been present on the live shark is missing. The first radial is far broader than the others and there is no evidence of it being jointed. While none of the subsequent radials have preserved joints there are several disarticulated distally pointed radial fragments scattered around the fossil. This, along with examination of other

hybodont pelvic girdles, indicate that all radials other than the first were jointed at least once.

2.2.4 Discussion

Although the teeth are only preserved as imprints the tooth morphology in specimens A and B appears to be virtually identical. There is some difference in skeletal morphology, notably in the general shape of the palatoquadrate and scapulacoracoid but this could be due to taphonomic alteration and is not sufficient to assign the two specimens to different species. Specimen C has no teeth but its similarity in both size and general morphology would allow a tentative assignment to the same species as specimens A and B.

Tooth morphology in specimens A and B is short, broad and pyramidal with a pronounced peg visible on the labial side. This would indicate a lonchidiid shark. Other lonchidiid sharks, such as *Lissodus africanus* (Brough, 1935) and *Lissodus cassangensis* (Antunes et al., 1990), have been found in the Lower Triassic of Africa. The occipital region in the current specimens is relatively short in comparison to *Hybodus basanus* (Maisey, 1982) but can not be compared with either *Lissodus africanus* (Brough, 1935) or *Lissodus cassangensis* (Antunes *et al.*, 1990) both of which have poorly understood cranial morphology.

In comparison to some Mesozoic hybodonts described by Maisey (1982), the specimen has a long and slender scapulacoracoid, but it is still comparable to that of *Hybodus fraasi* (Maisey, 1982) and and *Polyacrodus twitchetti.* The scapulacoracoid described in *L. cassangensis* (Antunes *et al.*, 1990), is much broader than that in the

current specimens. The figure in Antunes *et al.* (1990) however, appears to show both halves of the scapulacoracoid superimposed on top of each other giving an artificial impression its broadness. The structure and placement of the basals in specimen A is remarkably similar to that of *Lissodus cassangensis*.

While insufficient for a definite assignment to *L. cassangensis* the above suggests an assignment of Specimens A-C to *L.* aff *cassangensis* to be appropriate.

Specimen D consists of a pelvic fin. There is no other material associated with the fossil that would allow the positive identification of this shark to generic level. The size of the pectoral fin would suggest a shark that was considerably larger than specimens A, B and C. Specimen D may be an adult and it is possible that the other specimens represent juveniles of the same species but without either teeth or other preserved skeletal morphology it is not reasonable to assign them to the same genus. For this reason Specimen D is assigned to Hybodontoidea indet.

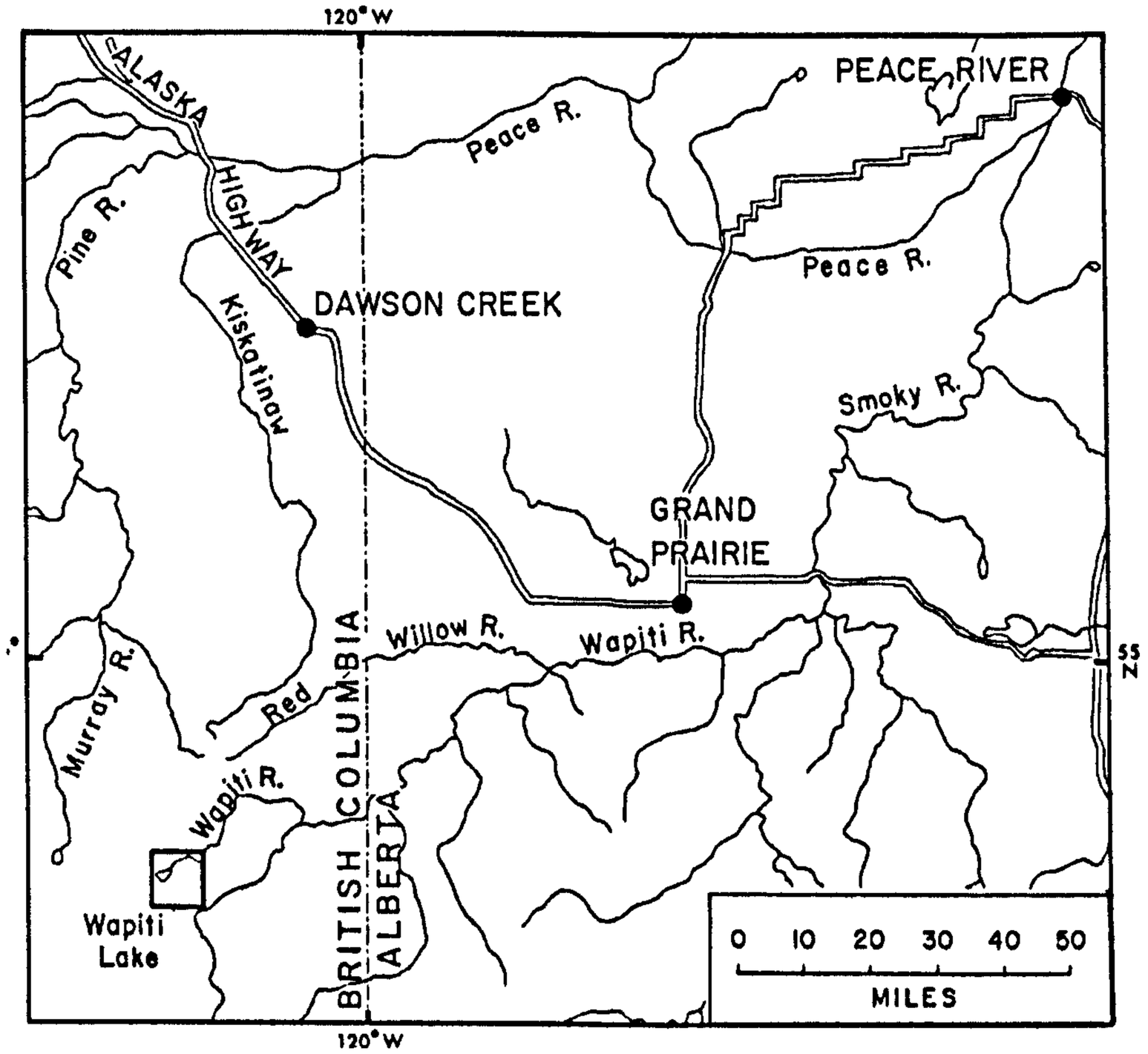
2.3 The hybodont fauna of the Lower Triassic of Wapiti Lake, Canada

2.3.1 Introduction

The geology and fauna of Wapiti Lake were preliminarily described in Schaeffer and Magnus (1976) and Neuman (1992). In brief the fossil fishes come from the lowest section of the Sulphur Mountain Formation called the Vega-Phroso Siltstone member. Neuman (1992) considered most of the fossil fish to be Smithian in age but subsequent studies (Orchard and Tozer 1997, Mutter Pers. Comm. 2004) have revealed the Vega-Phorso Siltstone Member to be Induan to Olenekian in age with the majority of the fossil fish coming from the Olenekian. The Lower Triassic sediments from the Wapiti Lake area were more likely deposited in a "relatively shallow-water, deltaic to shallow continental shelf environment, in an initially transgressive (Phroso-like strata), but subsequently regressive (Vega-like strata), sea influenced by turbidity and/or storm generated currents" (Neuman 1992).

2.3.2 Materials and Methods

The specimens described in this section are stored in two separate institutions. Specimens with the prefix TMP are stored in the Royal Tyrrell Museum of Paleontology in Drumheller while those with a UAE prefix are stored in the University of Alberta Earth Sciences collection. All photographs where taken using digital cameras and normal light.



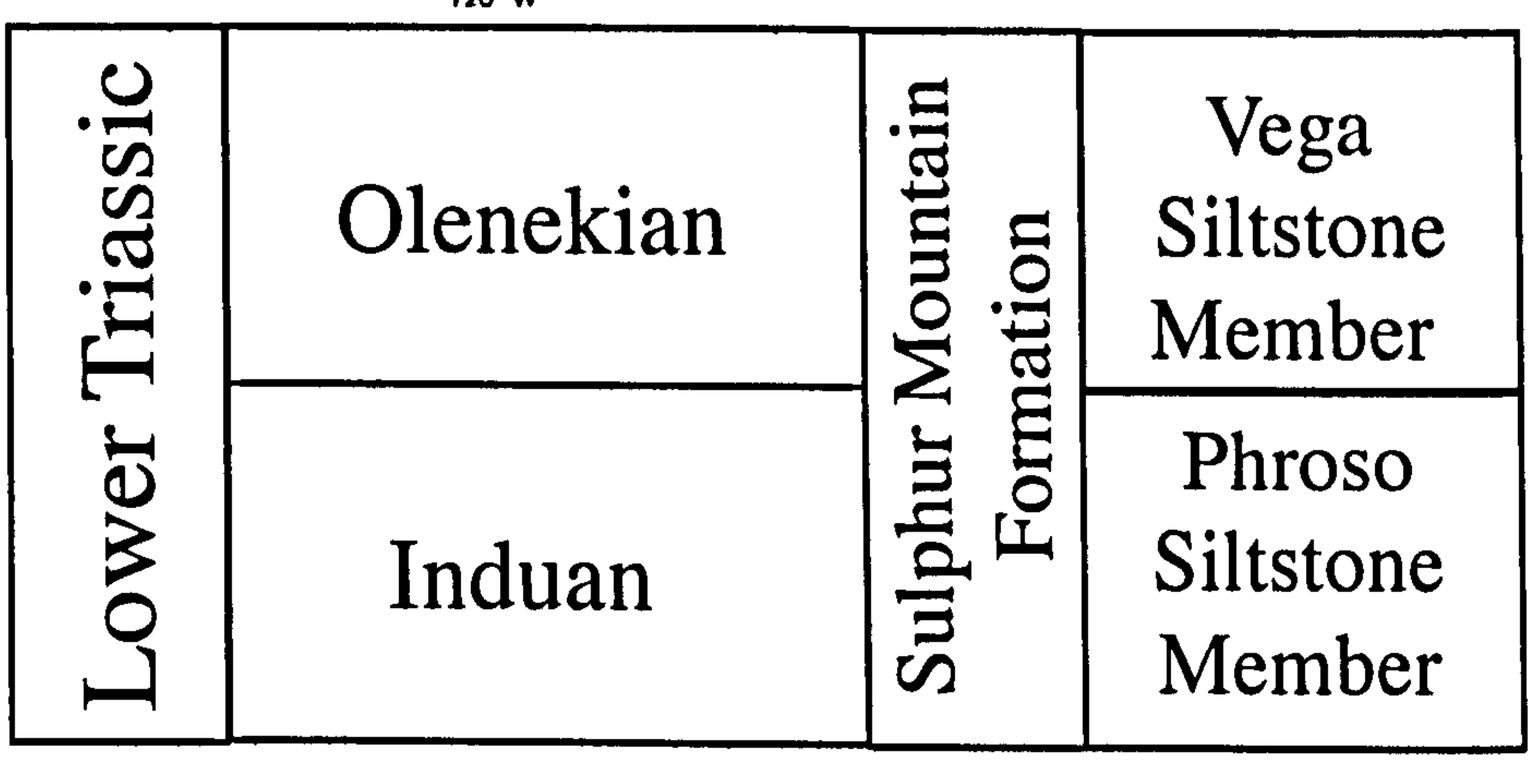


Fig 2.23. Locality and stratigraphy of WapitiLake

2.3.3 Systematic Palaeontology

2.3.3.1 *Wapitiodus wapitiensis*

Cohort Euselachii Hay, 1902

Superfamily Hybodontoidea Owen, 1846

Genus *Wapitiodus* nov. gen.

Diagnosis: Body short and robust, dorsal finspines comparatively gracile; anterior teeth with high acuminate cusps and concave crown base; main cusp centrally located with no lateral cusps; ornamentation consists of dense and fine ridges originating from crown-root junction and ascending the crown but not reaching the longitudinal crest; posterior teeth lower and wider than anteriors; main cusp very reduced or absent with no lateral cusps; ornamentation consists of sparse and coarse ridges originating from cusps and terminating at crown/root junction, ridges bifurcating; root of equal or greater depth than crown labial peg poorly defined or absent; lingual peg absent.

Etymology: Named for type locality

Type Locality: Olenekian, Wapiti Lake, British Columbia

Type Specimen: TMP 97.74.10

Species *wapitensis* nov. sp.

Diagnosis: as for genus.

Etymology: Named for type locality

Type Locality: Olenekian, Wapiti Lake, British Columbia

Type Specimen: TMP 97.74.10

2.3.3.1.1 Specimen TMP 97.74.10

The type specimen (TMP.97.74.10) is a fairly complete and well preserved hybodont body. The head including the jaws, hyomandibula and parts of the neurocranium have been preserved. The branchial arches have been damaged (both taphonomically and by subsequent preparation of the specimen). The scapulocoracoid is present though damaged. Portions of the pectoral fin (probably the propterygium) are present but the other basal elements and radials are missing. Both dorsal fins are preserved, as are the pelvic and anal fins. There is a partial vertebral column but the caudal fin is missing. The overall body shape (Fig. 2.24) is relatively shorter and more sturdy than most hybodonts that have a more fusiform streamlined body shape.

The counterpart is less complete only comprising the scapulocoracoid, anterior dorsal fin, pelvic fin and a partial vertebral column.

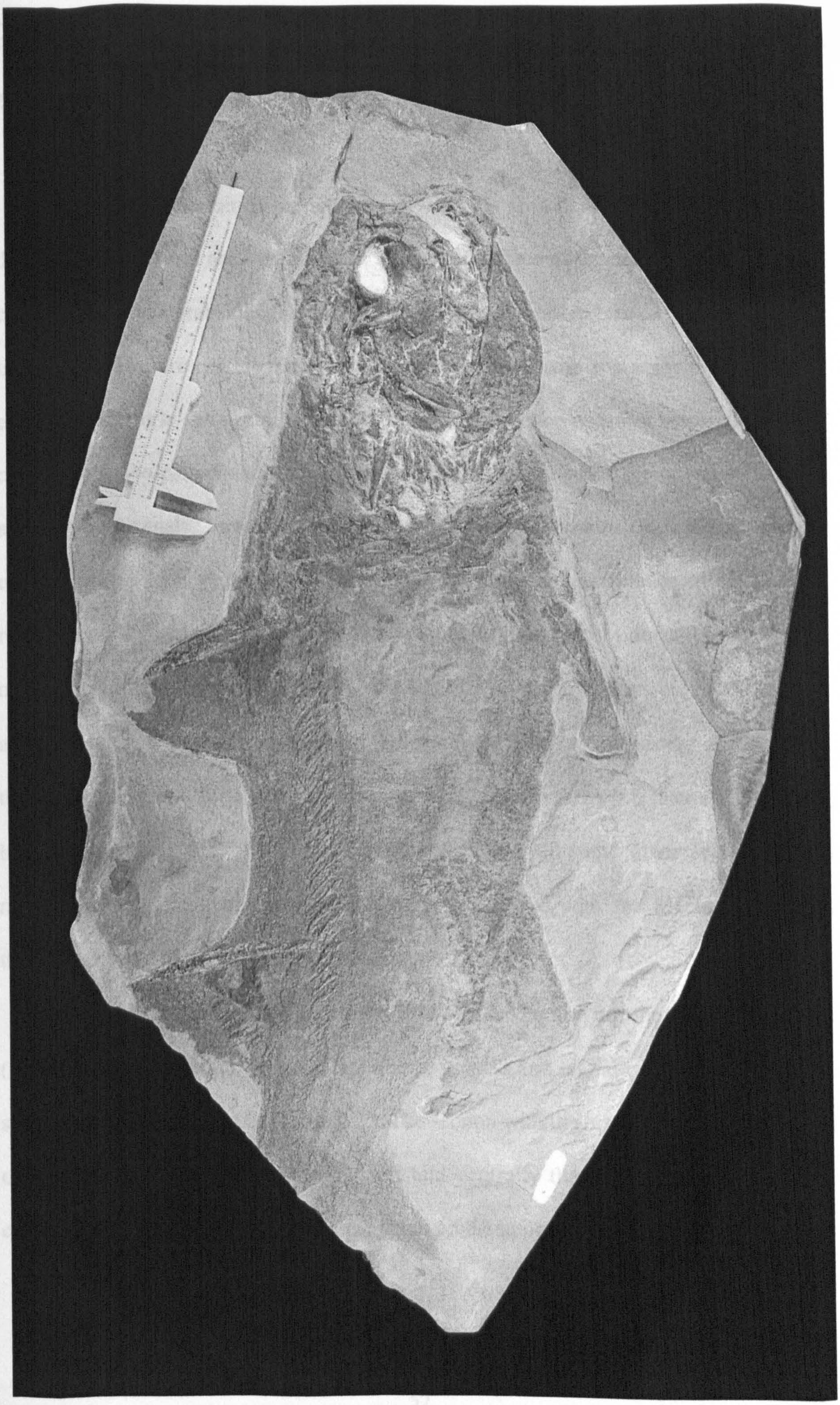


Fig. 2.24. *Wapitiodus wapitiensis* sp. no TMP 97.74.10

2.3.3.1.1.1 Neurocranium

The neurocranium is partially preserved. It is seen in lateral view obscuring all detail from the dorsal and ventral sides. The upper surface of the neurocranium has been crushed and the lateral side including the postorbital process and the lateral optic process is missing. The orbit is clearly visible as is a portion of the supraorbital crest, which extends posteriorly and ventrally before the preserved section ends just below the point of contact with the palatoquadrate. The lower portion that contained the lateral commisure and the jugal canals is missing. Extending behind the supraorbital crest (a layer usually covered with a large section of cartilage), just above the hyomandibular articulation is a roughly rectangular pit with a raised border around it that reaches dorsally to the height of the top of the orbit and the most ventral section of which borders the palatoquadrate and articulates with the hyomandibula. The hyomandibula curves postero-dorsally from the box structure to form a bow shape bar. In the centre there is a laterally projecting lump of cartilage that may be a disarticulated part of some other section of the neurocranium. The hyomandibula no longer articulates with the Meckels cartilage, though the point of articulation is still visible.

It looks as if the neurocranium was cleaved, removing the right lateral side (including the postorbital process, lateral otic process and lateral commisure), then was split along the line shown in Figure 2.25. The section with the orbit and preserved section of supraorbital crest tilted about 30° left and ventrally then the whole structure was covered and compressed, destroying the detail on the upper section of the skull.

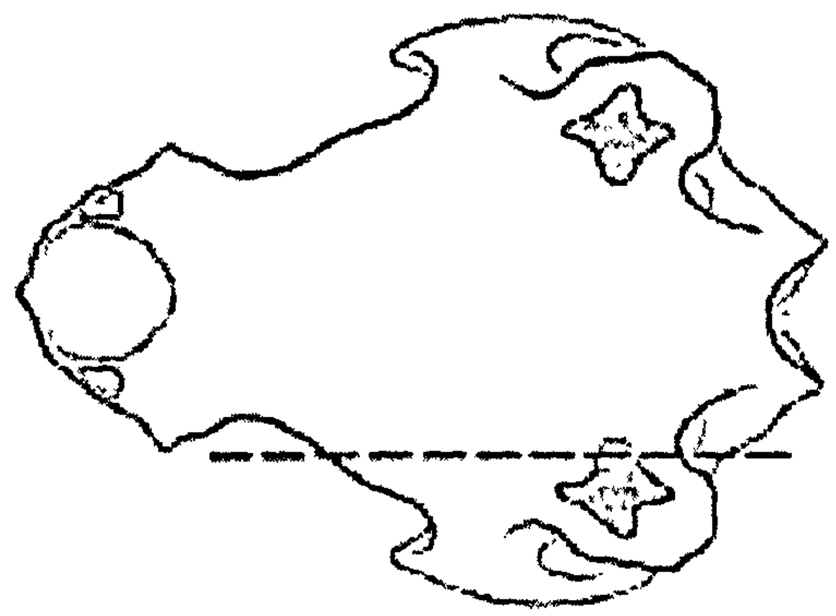


Fig. 2.25. Diagram showing line of split in skull of TMP 97.74.10, redrawn from Maisey 1982.

2.3.3.1.1.2 Palatoquadrate

The palatoquadrate is fairly well preserved. The anterior-most section of the palatoquadrate is either missing or obscured by the preserved section of neurocranium. At the front of the orbit the preserved section of the ethmopalatine process articulates with the palatoquadrate at the ethmoid articulation which then extends posteriorly under the preserved section of the post-orbital process. The palatoquadrate becomes visible again after the preserved section of the postorbital process and the fairly narrow quadrate flange curves posteroventrally downwards to meet the Meckel's cartilage. There are depressed areas on the lateral side of the palatoquadrate that could have been the adductor fossa. The far half of the palatoquadrate has also been preserved and is visible slightly ventrally to the near half. Most of the structure is obscured but it does have three partial rows of in-situ teeth, which will be described below.

2.3.3.1.1.3 Meckel's cartilage

The lower jaw is less well preserved and is no longer articulated with the palatoquadrate or the hyomandibula. There is little 3D preservation and the two halves of the jaw may have moved, sliding anteriorly or posteriorly to each other. There are two visible jaw joints at the rear of the specimen (from each side of the jaw) (one may be a hyomandibular articulation). The jaw is fairly deep. It has been crushed laterally obscuring detail but does have several in situ teeth in the anterior section.

2.3.3.1.1.4 Vertebral column

The preserved section of vertebral column has 31 preserved interdorsal elements each reclining posteriorly at an angle of 33° to the horizontal. They appear to become gradually smaller posteriorly

2.3.3.1.1.5 Dorsal Fins

The finspine on the anterior dorsal fin is fairly well preserved. The preserved section is 105 mm in length. The spine is inserted into the vertebral column at an angle of 72° to the horizontal. It has been split destroying the detail of the external ornamentation and there are no visible posterior denticles. The basal cartilage extends 47 mm along the spine and 48 mm behind its base. The fin webbing is only preserved on the dorsal side of the finspine with the extreme upper section being either missing or obscured by the matrix. The preserved section of webbing appears to extend at 32 mm behind the posterior end of the basal cartilage.

The posterior fin is slightly less complete with the posterior section of the fin webbing missing. The finspine is preserved to both ends and is 114 mm in length. It is inserted into the vertebral column at an angle of 73° to the horizontal. Like the anterior spine the dorsal spine has damage to the external layers, preventing the examination of the ornamentation, and it possesses no posterior denticles. The basal cartilage has been shifted dorsally post mortem.

There are six preserved radials, each at an angle of 49° to the horizontal and 108° to the basal cartilage. The basal cartilage extends 67 mm along the spine and 54 mm

behind its base. The radials are only partially preserved (the top end is missing) but appear to increase in length posteriorly (the most posterior one is the largest).

The webbing on the dorsal fin extends anteriorly 20 mm beyond the base of the finspine. The posterior section of webbing is incompletely preserved. The preserved section extends for 6 mm above the top of the finspine and 84 mm behind its base.

2.3.3.1.1.6 Scapulocorocoid

The scapulocoracoid is fairly damaged and the two halves are superimposed on top of each other. One half measures 140 mm in length. It is fairly slender but has a broader section, probably at the point of articulation with the pectoral fin (though it is no longer articulated). The widest point measures 23 mm.

2.3.3.1.1.7 Pectoral Fin

The pectoral fin has been damaged and disarticulated so that only one elongate basal element remains and no radials are present. There is another piece of cartilage attached to the scapulocoracoid that could have been a basal, most likely the propterygium (Fig. 2.26). The elongate element may have been the mesopterygium but there is no evidence of the metapterygium. The mesopterygium is elongate and thin at the proximal end but expands dorsally into a bulbous club shape. It is 91 mm in length and the bulbous section is 22 mm wide while the narrow section is only 13 mm wide.

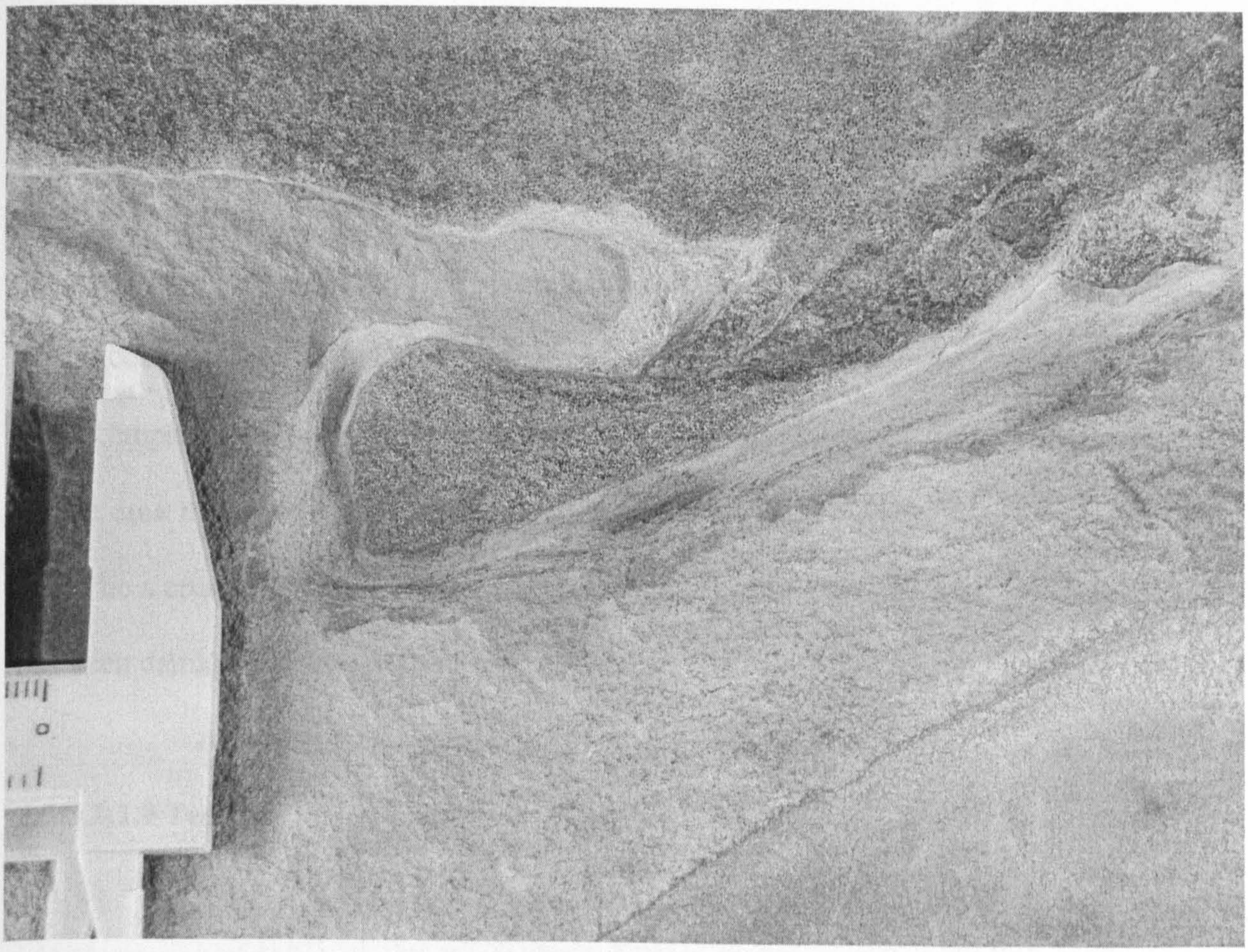


Fig. 2.26. Pectoral fin of TMP 97.74.10

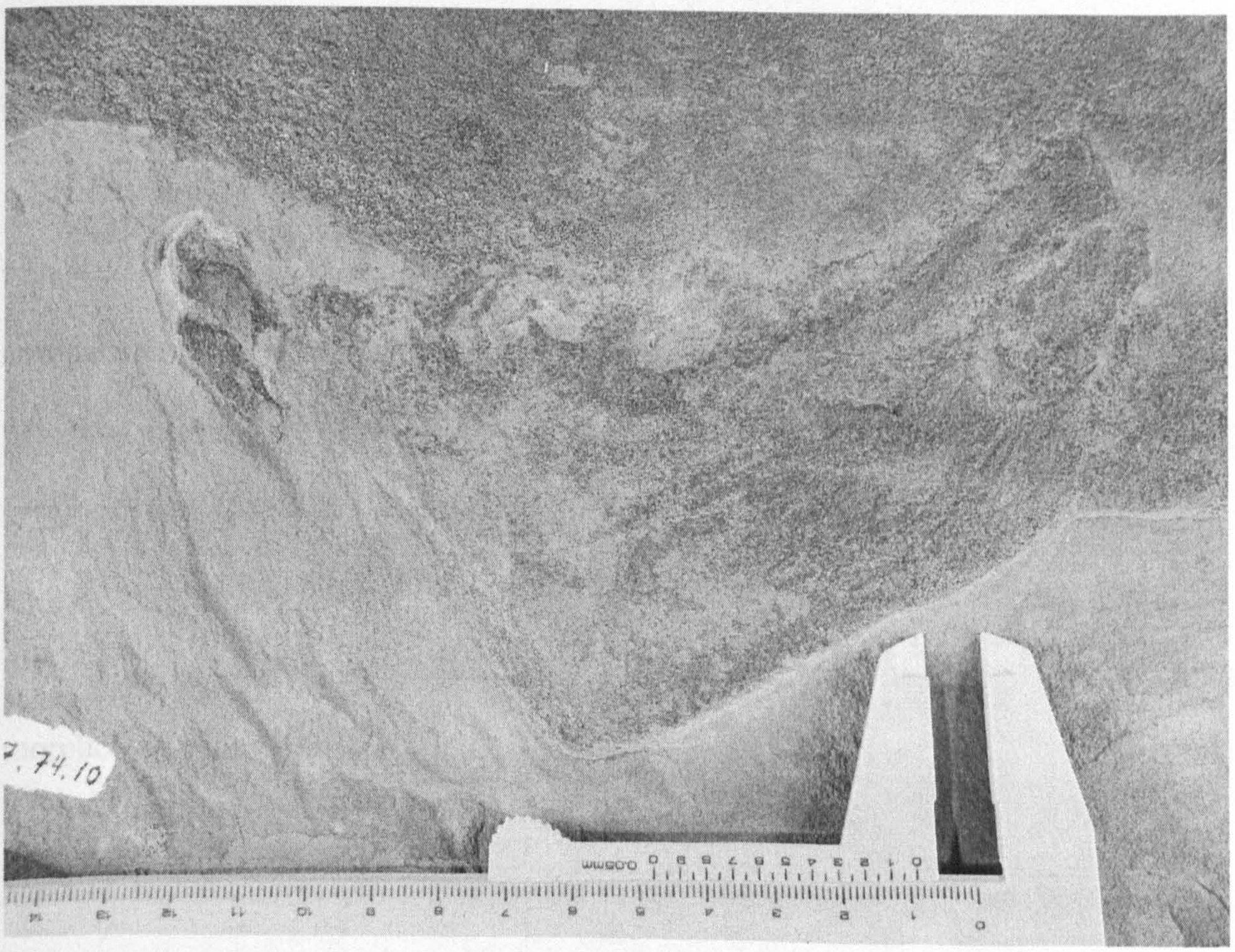


Fig. 2.27. Pelvic fin of TMP 97.74.10

2.3.3.1.1.8 Pelvic Fin

The pelvic fin is also quite poorly preserved. There are two visible basal elements, which could be both halves of the pelvic girdle. There are several visible radials but they are incomplete and it is impossible to determine their number or whether they are jointed. In the area that would have contained the metapterygium there is a vague shape that could be a crushed piece of cartilage and dermal denticles. The terminal clasper complex has been damaged and is hard to make out (Fig.2.27).

2.3.3.1.1.9 Teeth

There are three rows of preserved teeth (Fig. 2.28) on both the palatoquadrate and Meckel's cartilage. There is a pronounced monognathic heterodonty. The anterior theeth have a very high and acuminate main cusp with ridges stretching to the apex. The base of the cusp is remarkably concave and the tops of these teeth are acuminate. On the lateral side of the crown, reaching down slightly from the longitudinal crest is an unornamented area below which the ridges then begin and bifurcate basally. The root is very shallow in comparison to the crown. There appears to be little transition between the anterior and posterior morphology i.e. there are two distinct types of tooth morphology not a steady grading. There is little difference between upper and lower jaw dental morphology.

The posterior preserved teeth show the general described durophagous morphology. They have a very mesio-distally elongted, long crown with a low to non-

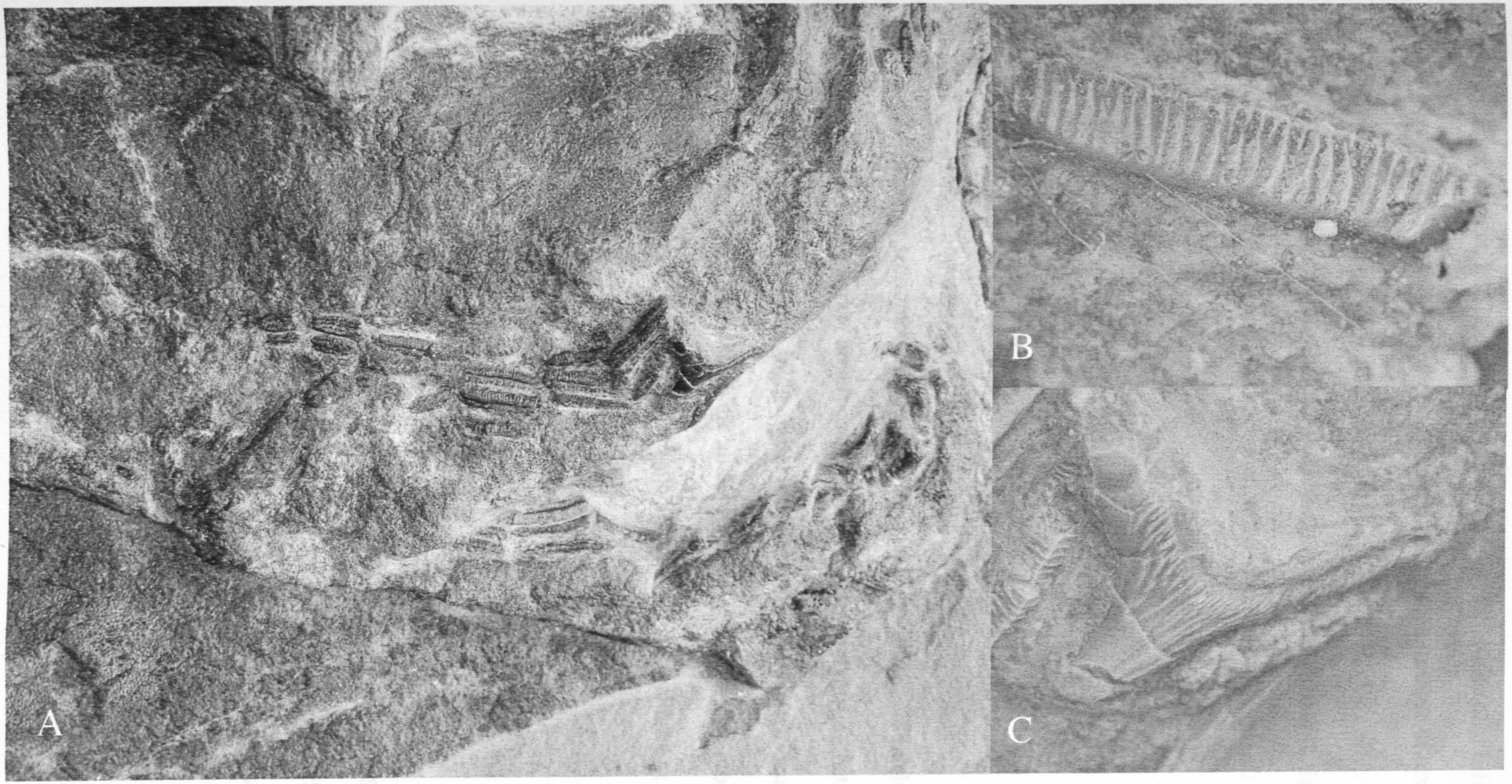


Fig. 2.28. Teeth of TMP 97.74.10. A. Overall view of mouth, B. posterior tooth, C. anterior tooth.

existent main cusp and no lateral cusps. There are basally pronounced bifurcating ridges. The root is roughly equal to crown in depth and possesses a number of irregular foramina scattered randomly on the root.

The unique dental morphology and arrangement, combined with the short, robust body shape implies that the current specimen is a new genus of hybodont.

2.3.3.1.2 Specimen UAE 17932

2.3.3.1.2.1 Vertebral Column

The anterior section of the specimen has clearly visible interdorsals but the posterior section has a darker area (possibly caused by water damage) that obscures the detail of the vertebral column. In the preserved area there are 17 interdorsal elements visible, posteriorly reclining, which are all approximately 21 mm long though they seem to decrease in size towards the rear of the specimen. They are reclining at an angle of 50° to the horizontal.

2.3.3.1.2.2 Dorsal Fin

The finspine is 81 mm long and is 6 mm wide at its widest point. It is inserted into the vertebral column at an angle of 77° to the horizontal. The exterior surface of the spine has been damaged obscuring the ornamentation. There are no preserved posterior denticles that are usually found on hybodont finspines.

The visible fin webbing extends for 19 mm anteriorly and 74 mm posteriorly from the spine. The webbing continues after the apex of the spine along the same angle for 34 mm and the overall height of the fin (from the base of the basal cartilage) is 101 mm. There are at least 9 visible supporting radial each longer than the ones anterior to it. The radials all lie at the same angle of 48° to the horizontal. The shortest visible radial is 7 mm while the longest is 25 mm.

2.3.3.1.2.3 Pelvic fin

There is a large lump of cartilage directly below the finspine that may have been a portion of the pelvic fin but it has been too badly damaged to make out the structure. There are also a number of visible denticles on the specimen but they have been badly eroded and it is not possible to make out the 4 pronged acuminate projections described by Schaeffer and Magnus that allowed them to assign their specimen to *Palaeobates*.

2.3.3.1.3 Museum Display Specimen (UAE 19199)

The specimen is preserved from the rear of the neurocranium to midway along the caudal fin and measures 244 mm in length (Fig 2.29). Total body length probably didn't exceed 300 mm. Despite the large section of the body that has been preserved there is little detail as preservation of most structures was very incomplete.

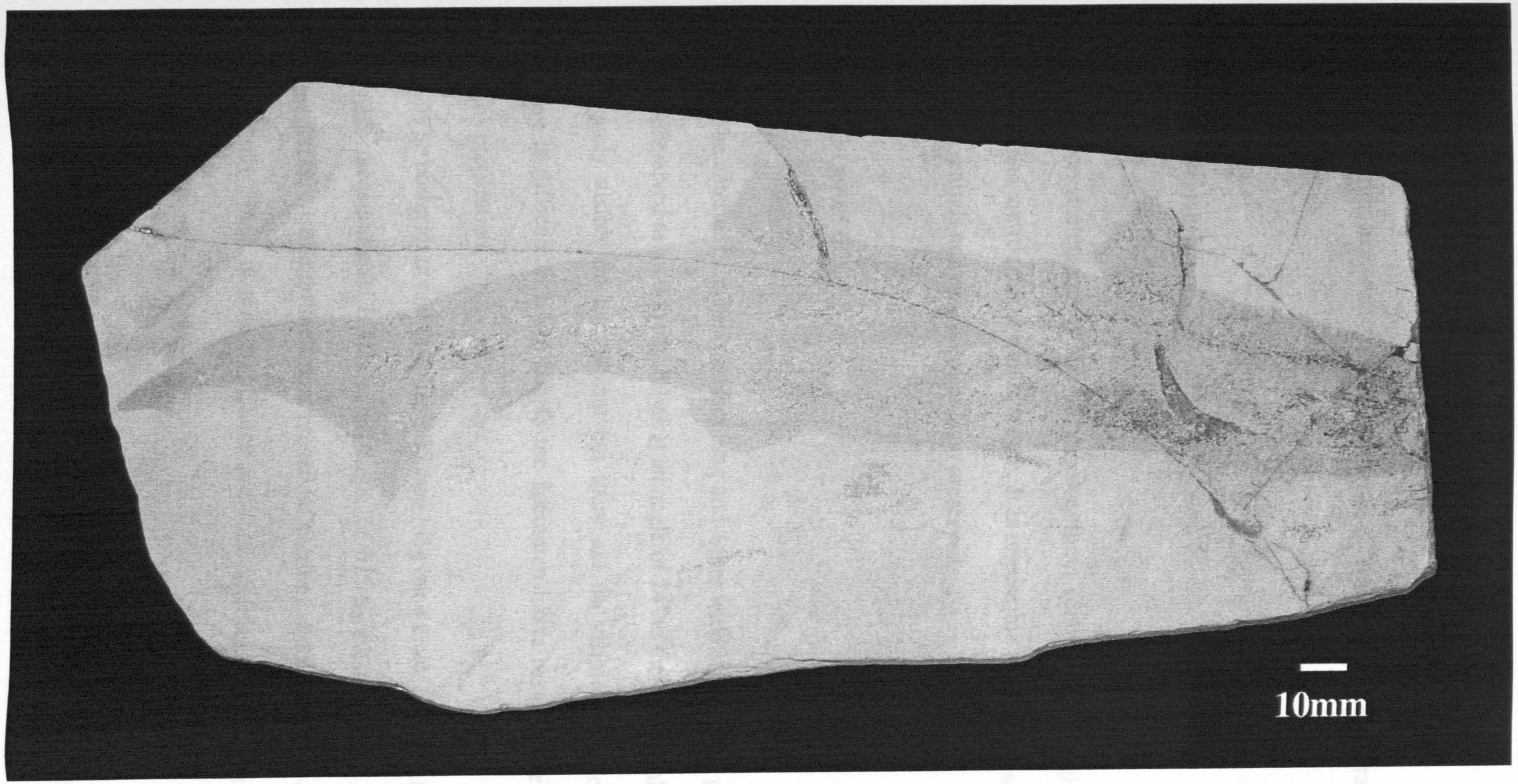


Fig. 2.29. *Wapitiodus wapitiensis* UAE unnumbered museum display specimen

2.3.3.1.3.1 Cranial anatomy

The head section has been crushed obscuring all detail of the neurocranium, jaws and branchial arches.

2.3.3.1.3.2 Vertebral column

The interdorsal elements of the vertebral column recline at an angle of 18° to the horizontal and are roughly 3 mm in length. It is impossible to make an accurate count of them. Basiventrals and ribs have not been preserved.

2.3.3.1.3.3 Dorsal fins

The anterior finspine is 20 mm long and 4 mm wide at its widest point though it is largely preserved as an imprint. It lies at an angle of 74° to the horizontal. Vertical ridges are vaguely visible on the imprint but there are no visible posterior denticles. Fin webbing is difficult to make out as the specimen has a resin painted outline (from previous preparation)

The posterior dorsal finspine is 17 mm long but a crack along its length prevents a thickness measurement. It lies at an angle of 61° to the horizontal. There is some ornamentation visible on the upper preserved section, which contains vertical lines but much of the spine is missing. There are four visible radials. These are however incomplete.

2.3.3.1.3.4 Scapulocorocoid

Part of the scapulocoracoid has been preserved, but both distal and proximal ends are missing. The preserved section is roughly horn-shaped, expanding towards the lower section and measuring 25 mm in length.

2.3.3.1.3.5 Pectoral fin

The pectoral, pelvic and caudal fins are too badly damaged to yield any useful information. Three lower radials are visible in the lower lobe of the caudal fin.

2.3.3.1.4 Discussion

There are several factors that distinguish *Wapitiodus* from other hybodonts. The general outline is shorter than that of most hybodonts with a blunter snout and a less deeply inclined dorsal surface. There have been few full-bodied hybodonts of comparable size and none found in the Lower Triassic. Holzmaden is the most obvious locality that has yielded relevant material, namely several complete or almost complete specimens of *Hybodus hauffianus* from the early Jurassic. All of these specimens show a greatly more elongate and fusiform body shape than the current specimen (Duffin 1997). There have been other similarly sized hybodont specimens including *Hybodus fraasi* (Brown 1900) and a few partial specimens from Monte San Giorgio (Rieppel 1981) but none display the

short and robust body morphology seen in the current specimen. Most smaller hybodont also have a more fusifom shape than the current specimen.

In addition to the general body morphology there are several skeletal characters that distinguish *Wapitiodus* from other hybodonts. The rostral bar is less pronounced than that seen in Fig. 2 of Maisey (1982) but the nasal capsule is larger and extends further back into a roughly oval shape. In comparison to those seen in Fig. 7 of Maisey 1982 the palatoquadrate is of average length and height but with a narrower quadrate flange and a reduced jaw joint. The jaw is fairly deep (roughly midway between *Egertonodus. basanus* and *Acrodus nobilis*, Maisey 1982, fig. 7).

No genus of hybodont has the same concave tooth base or blunt, durophagous posterior teeth seen in this specimen. The anterior teeth on the current specimen bear a very superficial resemblance to other hybodonts e.g. *Polyacrodus sp.* A, (Rieppel *et al.* 1996). *Polyacrodus keuperianus* (Winkler, 1880), *Polyacrodus krafti* (Seilacher, 1943), *Polyacrodus cloacinus* (Quenstedt, 1858), *Polyacrodus raricosatus* (Agassiz, 1843), *Polyacrodus obtusus* (Agassiz, 1837), *Polyacrodus parvidens* (Woodward 1916), *Polyacrodus siversoni* (Rees, 1999),. *Polyacrodus balabansaiensis* (Nessov and Kazynyshkin, 1988) and *Polyacrodus prodigialis* (Nessov and Kazynyshkin, 1988) which are similar enough to be grouped together in a new genus, but there are enough differences to separate the Wapiti specimen from these, i.e. the prominent lateral cusps seen in the above species are not present in *Wapitiodus*, and the pronounced concavity at the base of the anterior teeth in the *Wapitiodus* are absent in the other species. The posterior teeth in *Wapitiodus* also differ from these species, which have posteriorly recurved cusps with the main cusp asymmetrically located on crown. In addition to this,

Wapitiodus has a barely noticeable main cusp and lacks the 1-3 pairs of lateral cusps found on the posterior teeth in the others.

The morphology of the posterior teeth, as well as the stratigraphic location (Lower Triassic), suggest a possible relationship between *Wapitiodus* and *Polyacrodus claveringensis*. Extreme anterior teeth have never been found for *P. claveringensis* making it impossible to be certain but it seems unlikely that these two sharks come from the same genus as there is only one family of anterior teeth on the current specimen with no evidence of grading to any tooth morphology similar to the anterior teeth found in *P. claveringensis*. The anterior tooth family on the current specimen have a high main cusp and do not seen to have any lateral cusps, unlike *P. claveringensis* whose anterior teeth have a lower main cusp and an asymmetrical distribution of 4 lateral cusps.

The museum specimen hybodont is preliminarily included in *Wapitiodus*, despite its poor preservation, due mainly to its slender dorsal finspine morphology. While this specimen does not appear to have the same short robust body shape shown in the type specimen this may be misleading as the outline clearly visible on the illustration is as a result of preparation for display rather than taphonomic processes. Even if the outline in the Museum specimen is accurate it may still be from the same species and the shape difference may be due to either sexual dimorphism or possibly a juvenile character. None of the characters that clearly separate the type specimen i.e. the rostral bar, the palatoquadrate or the jaw are preserved in the museum specimen. As previously stated the palatoquadrates in both TMP.97.74.10 and the museum display specimen are damaged preventing accurate comparison but they do both appear to be of a largely

similar shape. This cannot however be used to definitely distinguish these specimen from the others from Wapiti lake as they all also have damaged or incomplete palatoquadrates.

Comparison between *Wapitiodus* and *Palaeobates* sp. (Schaeffer and Magnus 1976), the only other previously described specimen from Wapiti Lake, is difficult as the original description is vague. The overall body shape is longer and thinner than both *Wapitiodus* specimens. Detailed skeletal comparison is impossible, as the *Palaeobates* specimen has no dorsal fins and very poorly preserved skeletal anatomy with the fins only being represented by "displaced patches of dermal denticles".

2.3.3.2 *Contrariodus wapitiensis*

Cohort Euselachii Hay, 1902

Superfamily Hybodontoidea Owen, 1846

Genus *Contrariodus* nov. gen

Diagnosis: Anterior teeth with low, triangular but not pyramidal shaped crown; main cusp centrally located and flanked by 0-1 poorly defined pair of lateral cusps, cusps symmetrical in distribution; ornamentation of very sparse ridges originating from longitudinal crest and terminating at crown/root junction, ridges not bifurcating; posterior teeth lower and wider than anterior teeth; main cusp centrally located with no lateral cusps; ornamentation even less prominent than on anterior teeth with ridges originating from cusps and terminating at crown/root junction, ridges may bifurcate; root less deep

than crown; specialised foramina absent; labial peg poorly defined or absent; lingual peg prominent.

Etymology: Named for type species

Type Locality: Carnian Peace River Formation, Canada

Type Species : *Contariodus contrariensis*

Type Specimen: GSC 105093

Species *wapitiensis* nov. sp.

Diagnosis: Species of *Contrariodus* with expanded projection or rear of dorsal fin webbing; relatively slender meckel's cartilage; possesses epichordal caudal fin supports; Teeth with low wide crown; no labial or lingual peg; no secondary cusps; ventrally extending, non-bifurcating ridges originating from the longitudinal crest.

Etymology: Named for type locality

Type Locality: Olenekian, Wapiti Lake, British Columbia

Type Specimen: UAE 46531

2.3.3.2.1 Specimen UAE 46527

Specimen UAE 46527 is a partially preserved vertebral column with both dorsal fins (Fig. 2.30). It includes interdorsals, a set of disarticulated fragments located ventrally

to the interdorsals (most likely the remains of the basiventrals and the ribs) and the remains of the pelvic girdle (though these have been badly damaged and are only identified as the pelvic girdle due to there position anterior-ventral to the posterior dorsal fin). The anterior fin has a partially preserved finspine and webbing but no basal cartilage while the posterior fin has preserved spine radials basal cartilage and webbing. The preserved section is 320 mm long.

2.3.3.2.1.1 Vertebral column

The preserved section of vertebral column has 23 preserved interdorsal elements each reclining posteriorly at an angle of 26° to the horizontal. They appear to become gradually smaller posteriorly and range in length between 42 and 29 mm.

The section ventral to the interdorsals has a jumble of preserved elements (probably ribs) but they are broken into small pieces and are too disarticulated to make out any useful detail.

2.3.3.2.1.2 Dorsal fins

The finspine on the anterior dorsal fin is only partially preserved. The upper section is present but the lower section (probably just over half the spine) is missing. The preserved section is 30 mm in length and 9 mm in width. The spine is inserted into the vertebral column at an angle of 53° to the horizontal. It has been split destroying the detail of the external ornamentation and there are no visible posterior denticles. The basal cartilage was not preserved (or is obscured by the preserved webbing). The fin webbing

is only preserved on the dorsal side of the finspine and begins just above the base of the preserved section (41 mm above the vertebral column). The preserved section of webbing appears to extend at least 9 mm but then is obscured by the matrix. There is an odd bump projection at the posterior end of the preserved section of webbing but this could just be due to the matrix.

The posterior fin is more complete. The finspine is preserved to both ends and is 79 mm in length and 15 mm wide at its widest point. It is inserted into the vertebral column at an angle of 61° to the horizontal. Like the anterior spine the dorsal one has damage to the external layers preventing the examination of the ornamentation and possesses no posterior denticles. The basal cartilage is only partially preserved (the posterior section is missing).

There are four preserved radials each at an angle of 49° to the horizontal and 78° to the basal cartilage. The radials are only partially preserved (the top end is missing) but appear to increase in length posteriorly (the most posterior one is the largest). From the anterior-most one to the posterior-most one the preserved sections of radial measure 8, 11, 16 and 18mm respectively. The second radial appears to be thicker than the others but it is possible that it is two radials squashed together.

The webbing on the dorsal fin extends anteriorly but is obscured by the matrix so it is impossible to tell exactly how far. The posterior section of webbing is incompletely preserved. The preserved section extends for 9 mm above the top of the finspine and 78 mm behind its base.

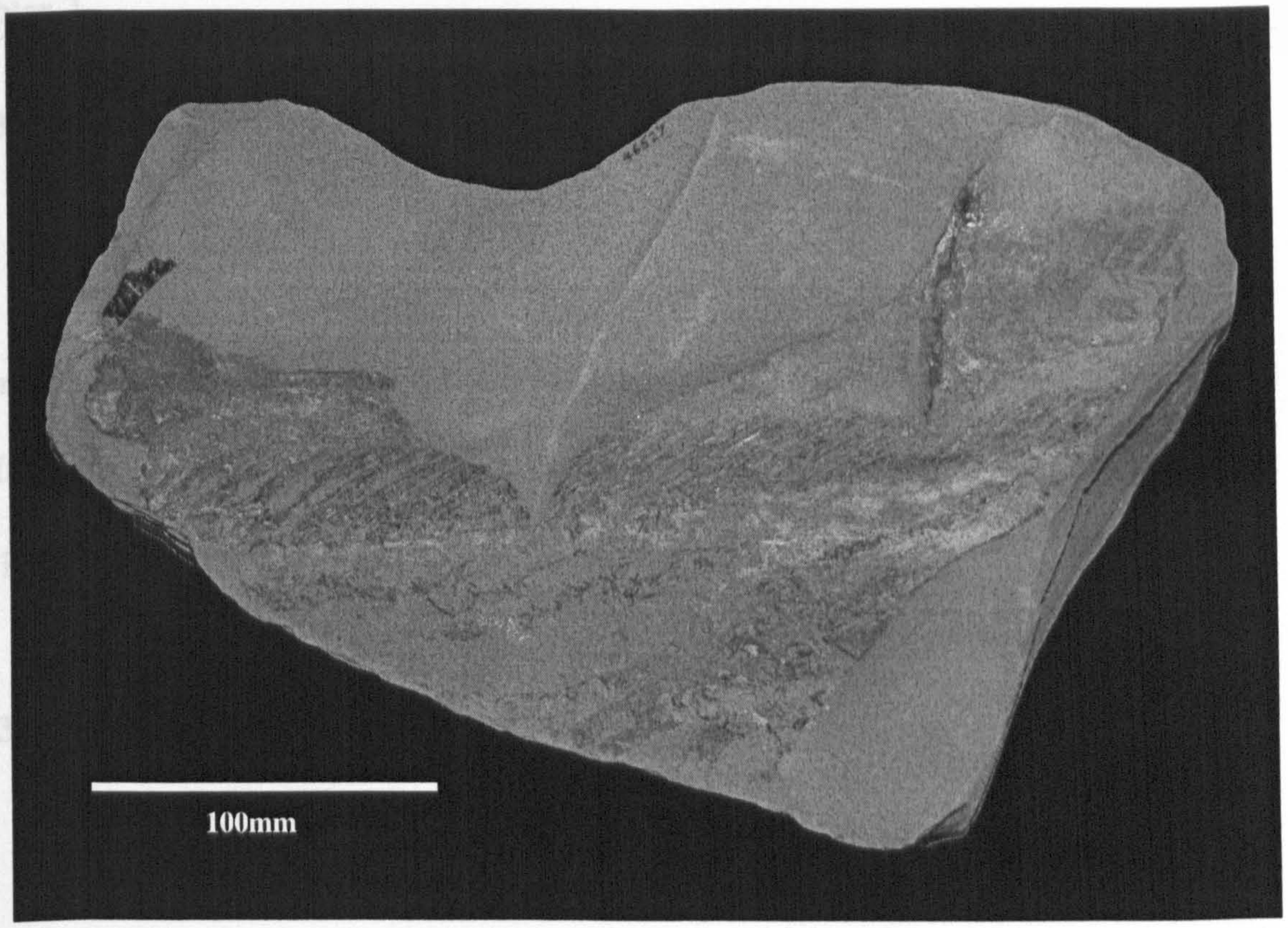


Fig. 2.30. *Contrariodus wapitiensis*,. UAE 46527.

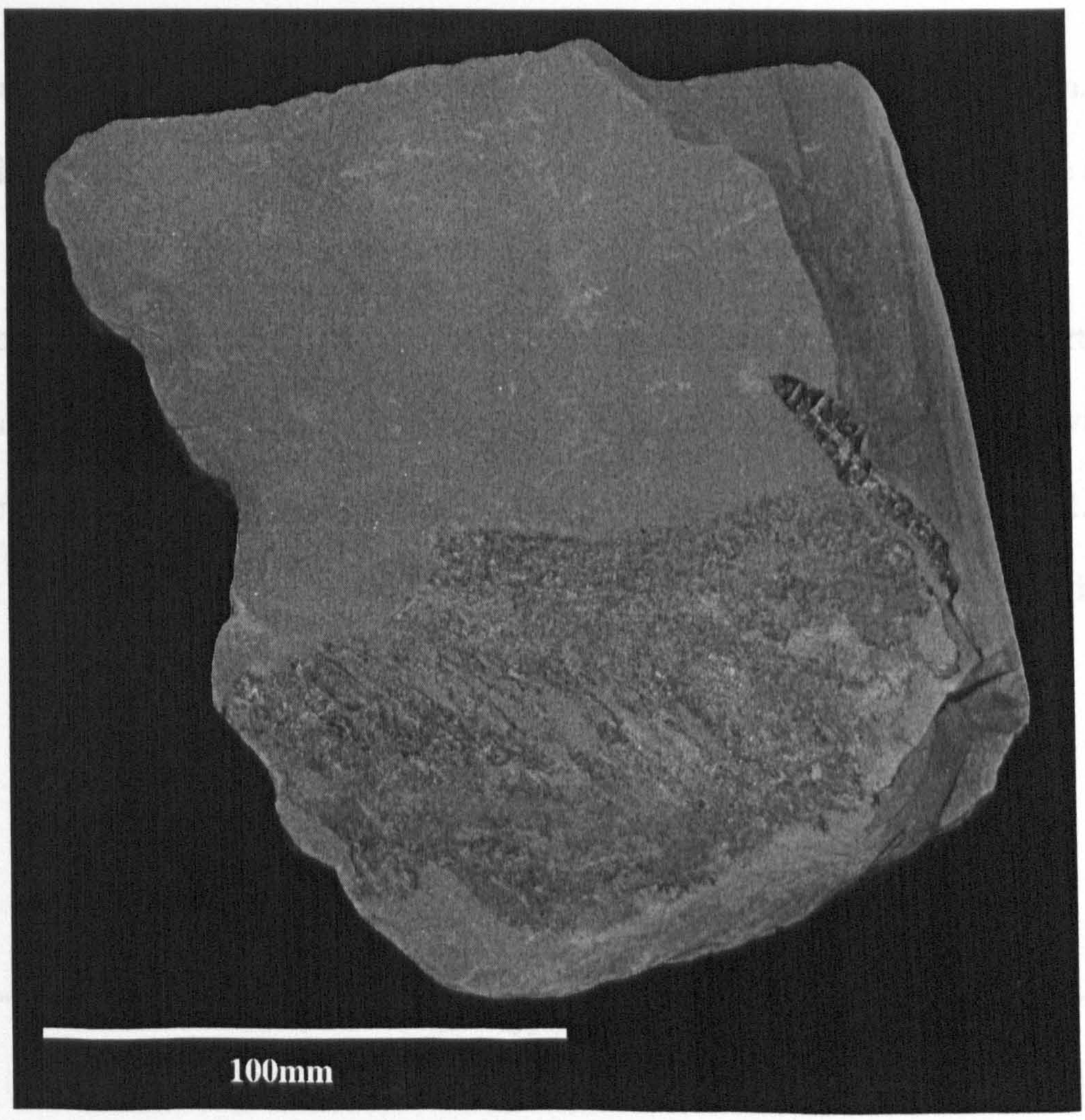


Fig. 2.31. *Contrariodus wapitiensis*, UAE 46528.

2.3.3.2.1.3 Denticles

There are a number of preserved denticles. None seem to have the four pronged extensions described by Schaeffer and Magnus (1976). The extensions in these denticles are far more rounded. The preservation is fairly poor and it is possible that they may have had posterior extensions that have since been eroded.

2.3.3.2.2 Specimen UAE 46528

Specimen UAE 46528 is a partially preserved anterior dorsal fin (Fig. 2.31).

2.3.3.2.2.1 Dorsal fin

The dorsal fin is very similar to the anterior fin described in the previous specimen. The finspine is 53mm in length (but the lower section is missing) and 100 mm wide at its

widest point, but would probably have been slightly wider. It is inserted into the vertebral column at an angle of 40°. Once again there is no preserved external detail and no visible posterior denticles. The basal cartilage in this specimen is partially preserved. The webbing extends for 11 mm behind the spine and has the same bump as seen in the previous specimen indicating that it was not the matrix defining its shape.

2.3.3.2.3 Specimen UAE 46529

Specimen UAE 46529 consists of a dorsal finspine (probable anterior dorsal) two fins (probably pectorals), a possible scapulacoracoid, a preserved section of vertebral column and a body outline (Fig. 2.32).

2.3.3.2.3.1 Finspine

The finspine is 63 mm long and 13 mm wide. It is flattened against the body so it is impossible to tell what angle it was inserted at. While damaged there is an imprint of the external structure which shows a series of fine striations descending the length of the spine.

2.3.3.2.3.2 Scapulocoracoid

The scapulocoracoid is only visible as a vague imprint which is 49 mm in length. It is very slender (2 mm wide) and is therefore only an outline of one side of the structure. The vertebral column extends for 27 mm anteriorly to the finspine and 114 mm posteriorly to it. There are two visible lines of interdorsals but the preservation is too unclear to get an accurate count.

2.3.3.2.3.4 Pectoral fins

The pectoral fins have a series of preserved radials that appear to originate from a single straight source (there are no preserved basal elements) and splay out like finger shaped projections. The radials appear to be thin at the base and then thicken towards the middle section before tapering at the end. The oddest thing is that they do not appear to be jointed in any way. There is an unpreserved section which may obscure joints but if it does then the joints are all in the same place regardless of the length of the radials. There are at least 14 radials visible in one fin. Radial 7 appears to be the longest with the others getting smaller laterally.

The preserved lengths of the radials are : 1) 17 mm, 2) 27 mm, 3) 34 mm, 4) 45 mm, 5) 52 mm, 6) 59 mm, 7) 62 mm, 8) 57 mm, 9) 53 mm 10) 47 mm, 11) 38 mm, 12) 21 mm, 13) 19 mm, 14) 9 mm. The fin webbing extends for at least 34 mm beyond the longest radial and 39 mm behind radial 14 in one fin.

2.3.3.2.3.5 Denticles

While poorly preserved some of the dermal denticles seem to have a similar structure to those seen is UAE 46527, while others at the rear of the specimen have a moderately long pointed central projection flanked by two shorter lateral projections.

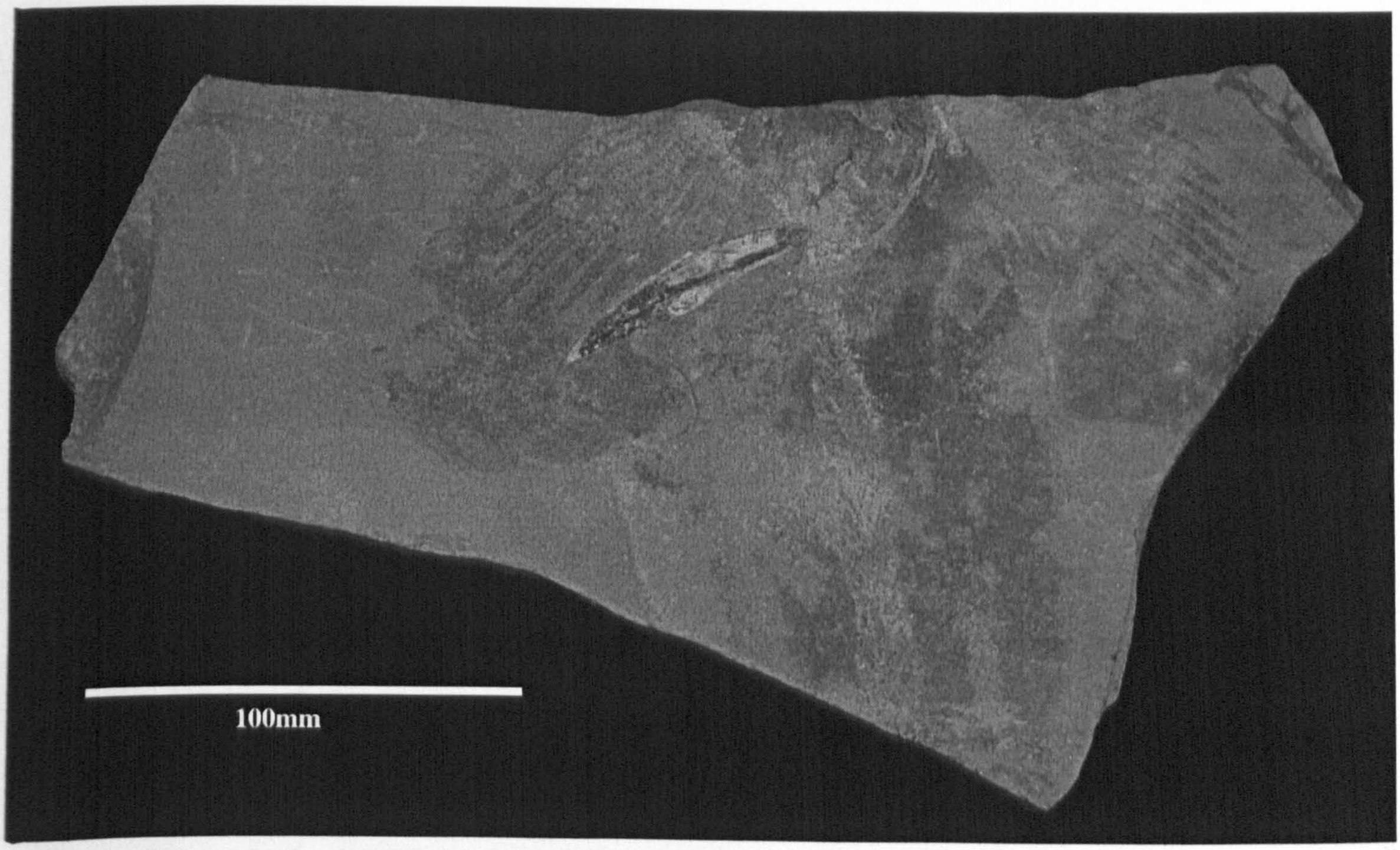


Fig. 2.32. *Contariodus wapitiensis* sp.no. UAE 46529.

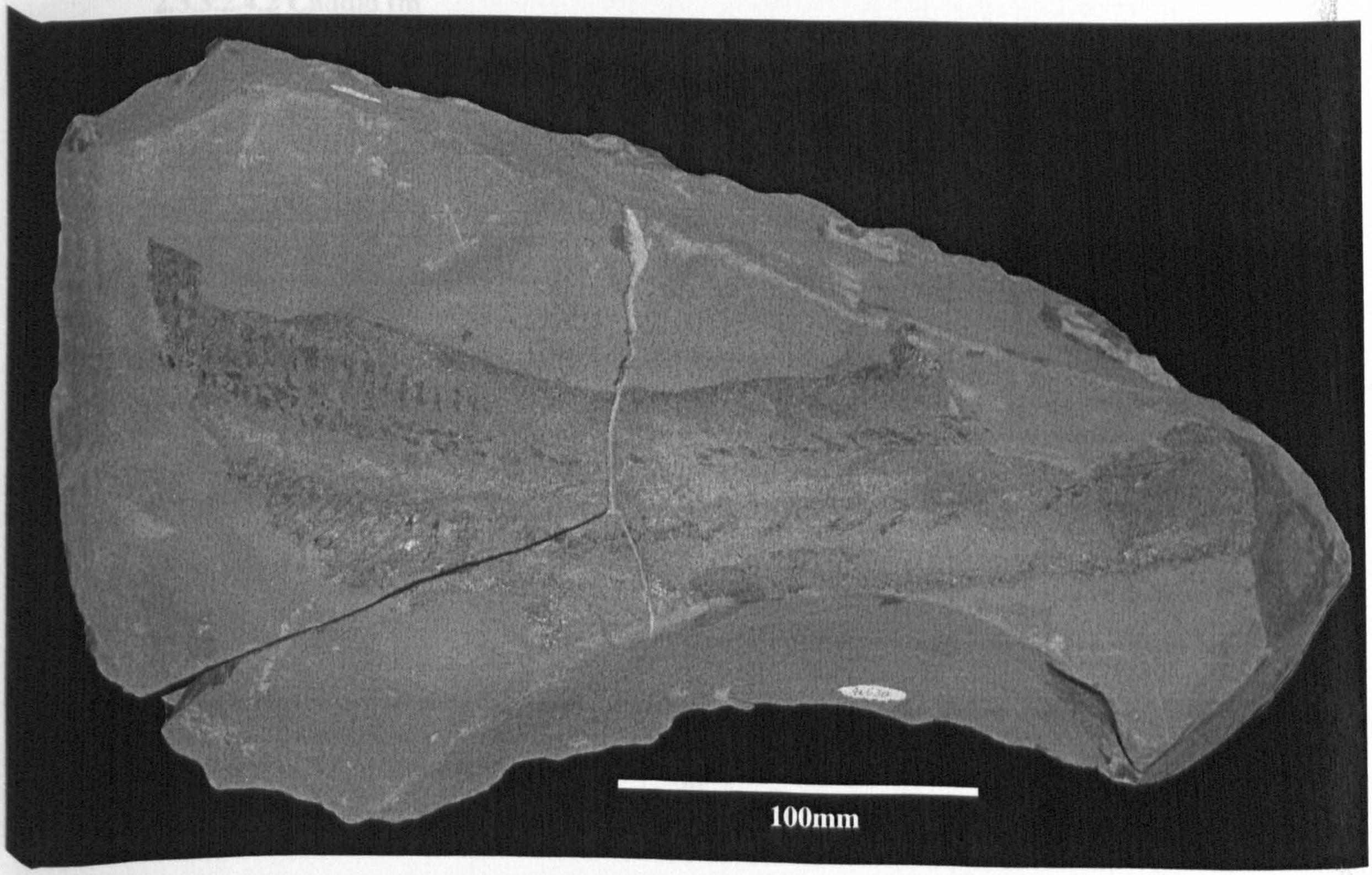


Fig. 2.33. *Contrariodus wapitiensis*, UAE 46530.

2.3.3.2.4 Specimen UAE 46530

Specimen UAE 46530 is a caudal fin (Fig. 2.33). From front to back the specimen measures 330 mm in length.

2.3.3.2.4.1 Vertebral Column

The anterior-most portion consists of a set of dorsally reclining interdorsal elements with associated basiventrals. The interdorsals reduce in size posteriorly and recline at an angle of 31° to the horizontal. The first visible epichordal fin supports (1-6) are only partially preserved (the lower section connecting to the interdorsals is missing). The vertebral column curves upwards at anterior end of the caudal fin.

2.3.3.2.4.2 Caudal fin

There are 17 visible epichordal supports. They appear to increase slightly in size posteriorly though they would probably eventually get smaller (the posterior-most section of the fin is not preserved. The smallest one is 17 mm in length (from the base of the preserved interdorsal) and the largest is 30 mm. Epichordal fin supports are an unusual feature in Mesozoic hybodonts with none of the specimens figured by Maisey (1982) possessing them. The basiventrals lie at equal but opposite angle to the horizontal as the interdorsals and extend into lower fin supporting elements at the same place. The lower elements lie at an angle of 46° to the horizontal. All lower elements have the lower

portion missing with the amount missing increasing posteriorly in each element. This makes it look like the elements decrease in size posteriorly (this may not be entirely misleading as it is the case in the majority of Mesozoic shark caudal fins). The preserved section contain 11 lower elements. While incompletely preserved it is clear that the bottom radials are far bigger and wider at the start of the caudal fin than the upper supporting elements. Dermal denticle morphology is identical to that seen in Specimen no. 46527.

2.3.3.2.5 Specimen UAE 46531

Specimen UAE 46531 is by far the most complete hybodont in the University of Alberta Wapiti Lake collection (Fig. 2.34). It consists of the lower jaw, a partial hyomandibula the rostrum, a poorly preserved branchial basket, a poorly preserved pectoral fin, a poorly preserved pelvic fin, vertebral column, both dorsal fins and a number of teeth.

2.3.3.2.5.1 Neurocranium

The possible section of rostrum is 21 mm in length. The extreme front end including the rostral bar is missing. The first preserved structure is a large hole, probably the nasal capsule, below which is a bulbous extension, which could be the ethmopalatine process. The structure curves back posterior to the bulbous process and extends into a longbow shape that would pass over the orbit. The rest of the neurocranium has been

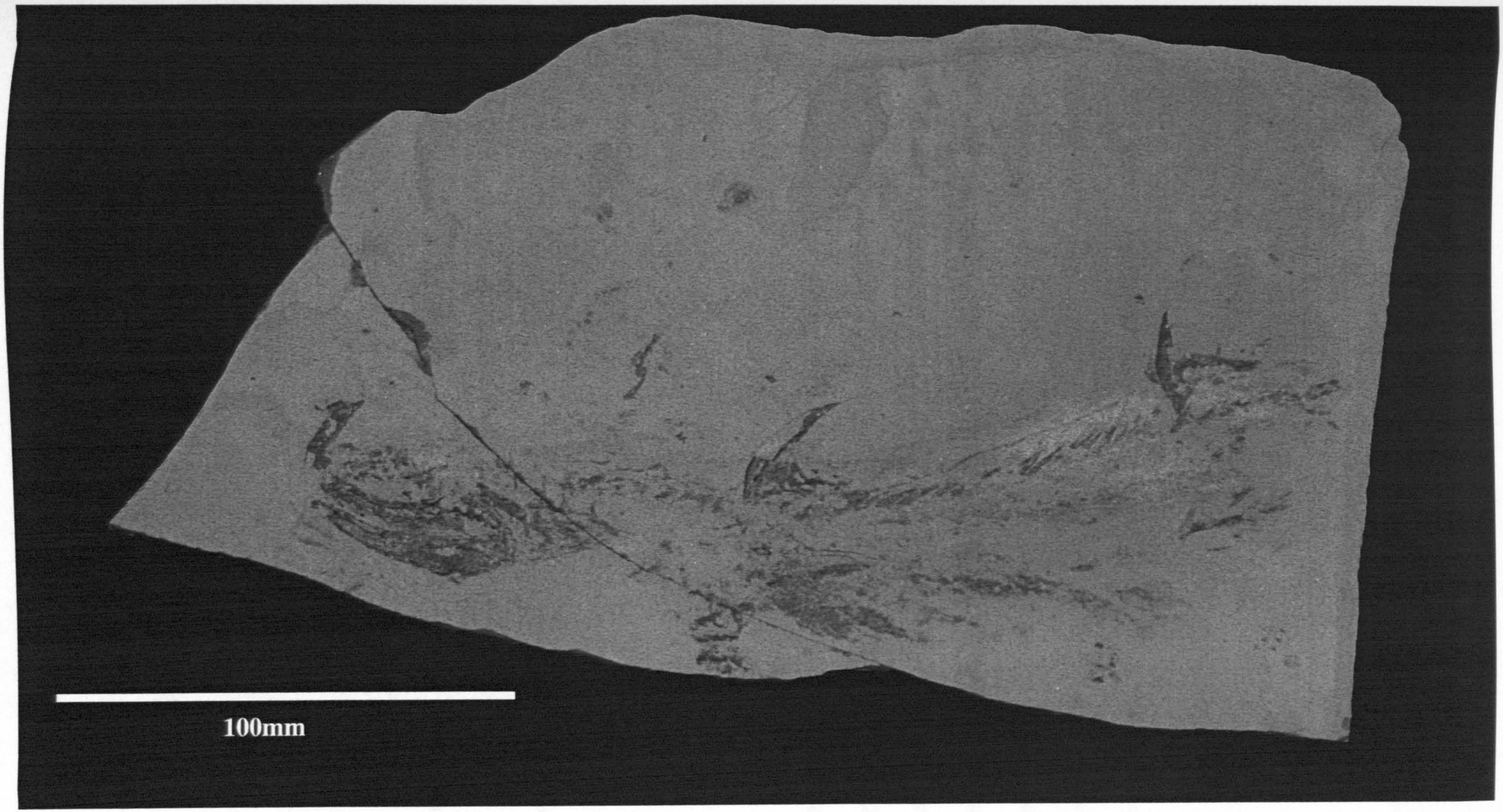


Fig. 2.34. *Contrariodus wapitiensis* sp.no. UAE 46531.

crushed beyond recognition and is visible only as a vague smear above the Meckel's cartilage.

2.3.3.2.5.2 Meckels's cartilage

The Meckel's cartilage is relatively slender. It is 11mm deep at its deepest point. It begins with a rounded anterior section then extends posteriorly with both the upper and lower edges curving ventrally, thickening slowly until its deepest point 33 mm from the anterior end. It then curves gently to meet at a rounded edge at the posterior. There is 3D preservation and evidence of muscle attachment areas from the middle to the rear section of the jaw. The second half of the lower jaw is also visible behind and slightly dorsally to the first half. The first section is seen in external view while the second section would show the inside of the jaw (though it is damaged and little detail can be made out).

Hyomandibula

Posterior and dorsal to the second section of the lower jaw is the hyomandibula. Its lower half is slender and extends for 3 mm before extending rapidly to the full thickness of the remainder of the structure. The entire hyomandibula is 17 mm in length. The lower section curves upward at the anterior end.

2.3.3.2.5.3 Branchial arches

The branchial skeleton has been quite poorly preserved. There are remains of three arches but there were likely two more. The entire preserved branchial basket measures 21 mm from front to back. There are 3 visible pharygobranchials with 3 more small ones (presumably from the other side of the basket) next to them. Below the pharyngobranchials are 3 posteriorly curved and ventrally extending epibranchials which join with 3 anteriorly curved ceratobranchials. The ceratobranchials have been crushed and are far less distinct than the epi and phayngobranchials.

2.3.3.2.5.4 Vertebral column

The interdorsal elements are indistinct between the rear of the cranium and the anterior dorsal finspine. There are only eight visible elements in this section and they have been smeared obscuring their shape. The shape of the interdorsal becomes clearer after this and there are 29 visible elements preserved between the anterior dorsal finspine and the end of the preserved section though they do become harder to make out after the posterior finspine. The interdorsal vary in size with the largest being 10 mm in length and lying at an angle of 30° to the horizontal. The vertebral column curves up towards the midpoint of the two dorsal fins indicating that the shark was bent post-mortem.

2.3.3.2.5.5 Dorsal fins

The anterior dorsal fin has a partially preserved finspine, which is 31 mm long and 5 mm wide at its widest point. It is inserted into the vertebral column at an angle of 50° to the horizontal. The central portion of the spine is missing but both extremities have been preserved as has a outline imprint of the missing section. The upper and lower preserved section exhibit the characteristic thin vertical ridges found on most hybodont dorsal finspines. The posterior denticles are once again missing.

The basal cartilage has been partially preserved. It shows the same curved shape as seen in the other anterior fins described.

There is some preserved fin webbing just above the apex of the basal cartilage and stretching to just posteriorly of it, but the webbing does not extend in front of or very high up the finspine.

The spine on the posterior dorsal fin is 20 mm long, 3.5 mm wide at its widest point and inserted into the vertebral column at an angle of 85° to the horizontal. Only a small portion of the posterior fin is missing and the vertical ridges are visible on much of the spine. No posterior denticles are visible. The outline of the basal cartilage has been preserved but a portion in the center was either not preserved or damaged.

The radials are very poorly preserved and only a few fragments from them remain. There are fragments from 5 radials visible but they are far too small and incomplete to establish the length and width they would have been.

The fin webbing is faintly visible extending for 15 mm above, and along the same angle as, the dorsal finspine and for 1-2 mm behind the last radial fragment.

2.3.3.2.5.6 Pectoral fin

The pectoral fin is poorly preserved and is only visible as a vague outline directly below the anterior dorsal fin. The entire length of the preserved section of the fin is 32 mm. The three basal elements are not visible but the shape of the preserved structure shows a stepped arrangement, which could be due to the unequal size of the basals. The top section (where the metapterygium would have been) is longer, though the full length probably includes where the radials would have extended to. The structure then shortens and curves gradually until the bottom (this probably comprises the meso- and propterygium, with associated radials).

2.3.3.2.5.7 Pelvic fin

The pelvic fin is also poorly preserved. The pelvic girdle is visible as a triangular shaped piece of cartilage below the posterior dorsal fin. This then extends into the metapterygium. Preservation is insufficient to make out any detail of the structure of the pelvic girdle or the individual basal segments of the metapterygium. There is no preserved mixipterygium though the extreme posterior section of the shark is missing.

2.3.3.2.5.8 Teeth

There are a number of teeth preserved within the specimen (Fig 2.35). The tooth found on the anterior-most section of the specimen has clearly been displaced as it is

embedded in the matrix with the cusp pointing into the lower section of the far half of the meckels cartilage. It has a wide but low crown with a main cusp that appears to be posteriorly recurved. This is however more than likely an artefact of the matrix covering the upper section of the posterior part of the crown. There is no evidence of any lateral cusps but the matrix may be covering the uppermost section of the lateral parts of the crown. There appears to be a series of bumps stretching along the face of the crown which may be associated with smaller lateral cusps. The face of the crown has been damaged so none of the ornamentation can be made out. The root is missing in this tooth and all other teeth preserved within the specimen.

The second visible tooth embedded is in situ in the anterior section of the front portion of the lower jaw. The crown is 1.2 mm long and is relatively low. There is only one visible cusp. The ornamentation of the tooth consists of series of ventrally extending ridges that do not appear to bifurcate. Since the root is not preserved (and the lower section of the tooth is damaged) it is impossible to tell if there is an overhang. There does not appear to be any well developed peg or basal projection. The bumps, seen on the previous specimen, were probably just the remains of the ridges.

There is another tooth preserved in lateral view. This tooth has an even lower crown indicating it came from a posterior part of the jaw. This too has ridges descending the crown and there is no evidence of lateral cusp or lateral peg/projections.

Finally there are two teeth preserved in longitudinal view. From this angle the ridges seem to project towards the apex of the crown, some joining to form a V shape on the longitudinal crest. At the apex of these V shapes there is a slight point but these points

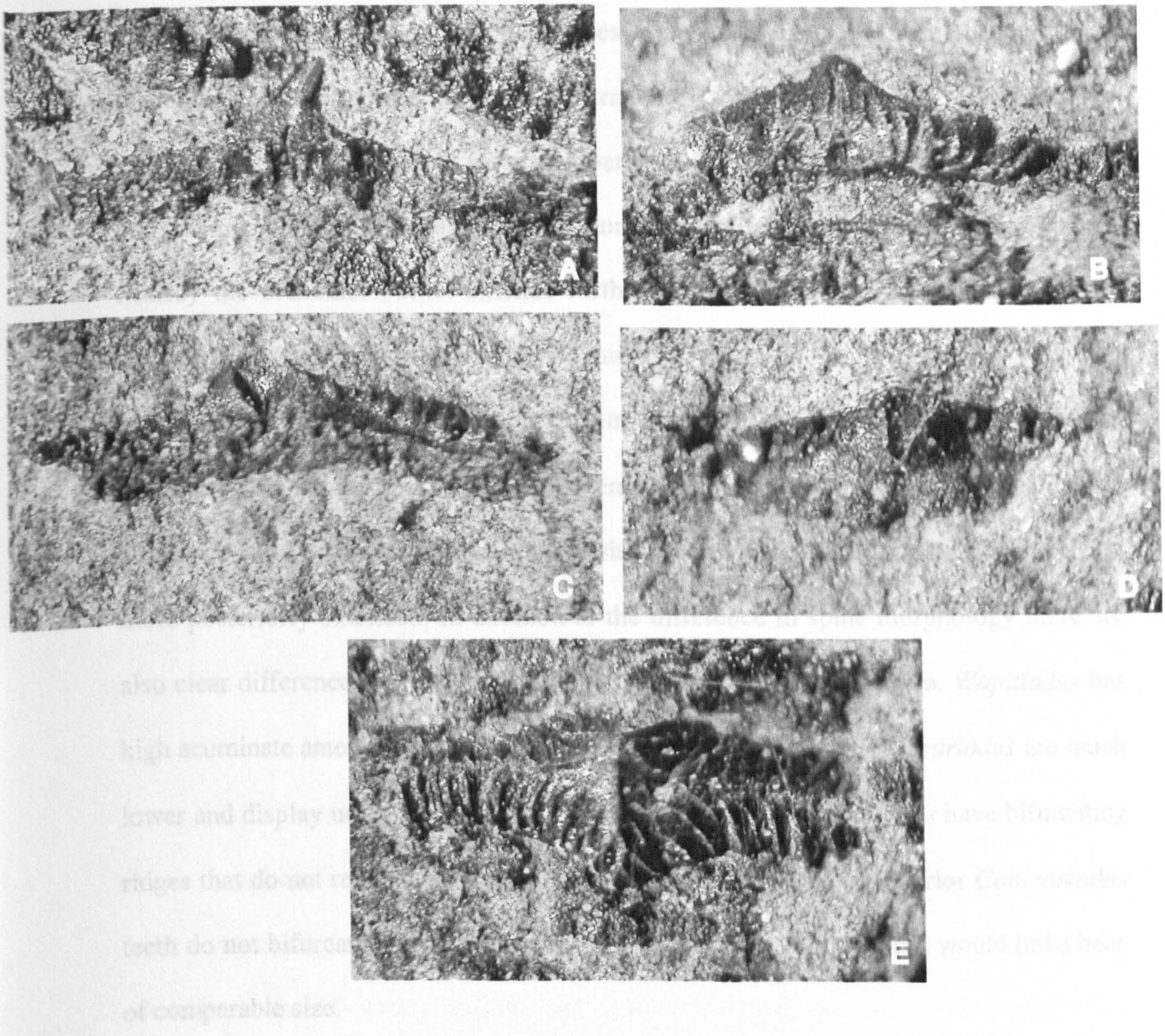


Fig. 2.35. *Contrariodus wapitiensis* sp.no. UAE 46531. Teeth.

are too low to be considered secondary cusps. At the center of the crown the tooth bulges out slightly but the bulge is too small and rounded to be considered a peg.

2.3.3.2.6 Discussion

The cranium in *Contrariodus* is best seen in UAE 46531. The structure is in lateral view and greatly resembles the illustration in (Maisey 1982 fig. 2C). The Meckel's cartilage is relatively slender when compared to those in Maisey (1982). This seems unusual for what was at least a partial durophagous feeder. In the reconstruction by Maisey the branchial basket extends further posteriorly towards the first dorsal fin indicating that the last few arches may be missing.

The *Contrariodus* specimens from Wapiti Lake are distinguishable from *Wapitiodus* as the posterior dorsal fin seems to have a different shape. The spines in *Contrariodus* are relatively more robust (shorter and thicker) and the basal cartilage is more posteriorly extended. In addition to the difference in spine morphology there are also clear differences in tooth morphology that separate the two genera. *Wapitiodus* has high acuminate anterior teeth with a concave bases while those in *Contrariodus* are much lower and display no concavity at the base. Anterior teeth in *Wapitodus* have bifurcating ridges that do not reach the longitudinal crest while the ridges on anterior *Contrariodus* teeth do not bifurcate and do reach the longitudinal crest. Both genera would have been of comparable size.

There is another hybodont species, *Contrariodus contrarius* (described by Johns *et al.*, 1997 from the Peace River area of North Eastern British Columbia) that has teeth

that bear some resemblance to UAE 46531. Both have anterior teeth with a low, triangular but not pyramidal-shaped crown. Sparse ornamentation of very sparse non-bifurcating, ridges originating from longitudinal crest and terminating at crown/root junction. The posterior teeth are lower and wider. The ornamentation on these is even less prominent than on anterior teeth with ridges originating from cusps and terminating at crown/root junction. The root is less deep than crown. The similarities justify this species inclusion within the genus.

2.3.3.3 *Polyacrodus* sp.

2.3.3.3.1 Specimen UAE 19191

Cohort Euselachii Hay, 1902

Superfamily Hybodontoidea Owen, 1846

Family Polyacrodontidae Glückman, 1964

Genus *Polyacrodus* Jaekel, 1889

Sp.

Specimen UAE 19191 is largely composed of a few long thin skeletal elements (probably ribs), a few unidentifiable pieces of scattered cartilage and one clear (but only partially preserved) tooth (Fig.2.36). All three of the long, thin skeletal elements have a longbow type shape but two of them have an odd opposite curvature at the end forming a S shape. None of the elements have a preserved distal end but the shape of the elements

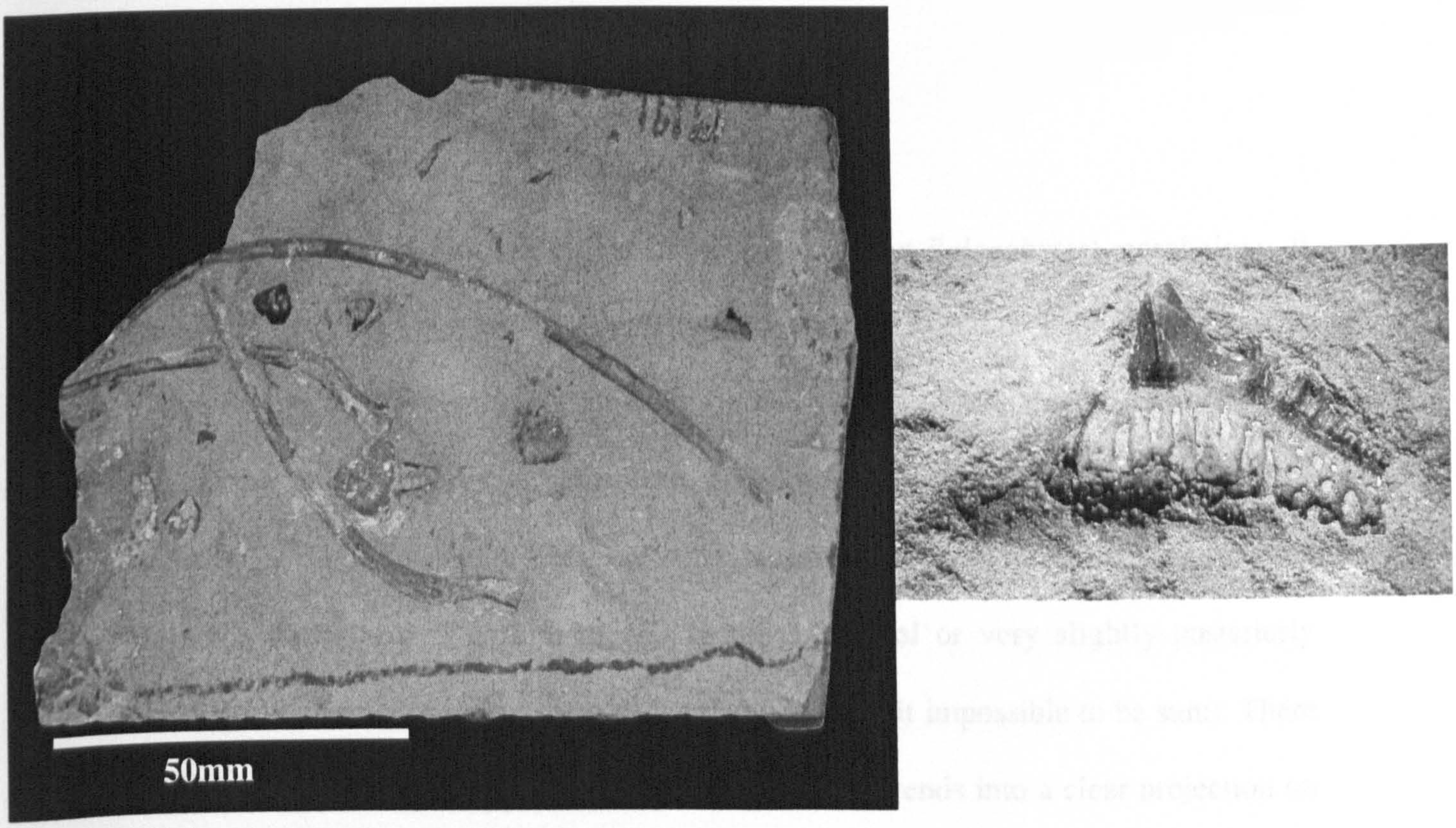


Fig. 2.36. *Polyacrodus* sp. UAE. 19191. Whole slab and close up of tooth

suggest that the distal end would taper to a point. The longest element measures 88 mm from end to end with the other two being 66 mm and 47 mm respectively. It is the two shorter ones that have S-shaped ends. If these elements are ribs it would indicate a shark that was at least 1.4-1.5 m in length.

2.3.3.3.1.1 Tooth

The tooth conforms to the general *Polyacrodus* (not *Palaeobates*) morphology. It is 6 mm in length but there is only partially preserved and would probably been closer to 10 mm originally. The crown in 2 mm high (though the apex of the main cusp is missing) and the root is approximately 2 mm deep. It is unclear whether the tooth is in labial or lingual view but the crown projects out at the bottom creating a slight overhang over the root. The main cusp is pyramidal and is either vertical or very slightly posteriorly reclining (the matrix obscures some of the detail making it impossible to be sure). There is only one ridge descending from the main cusp that extends into a clear projection on the (labial/lingual) face of the cusp. Besides this ridge the main cusp is free of ornamentation. Only one side of the crown has been preserved. On this side there are five visible lateral cusps each getting progressively smaller in size. There may be more very small lateral cusps at the far end giving a serrated like structure to the extreme ends of the teeth. Each of the lateral cusps also has one ridge descending from it and forming progressively smaller pegs. The crown is otherwise free of ornamentation.

The root as previously stated is 2 mm deep (as deep as the crown). In the centre it appears to have a single long row of regular foramina. By the second lateral cusp these foramina cease to be single, clear and long and degenerate into a series of seemingly

randomly placed circular foramina. The lower random foramina appear to be bigger than the upper ones.

2.3.3.4 Hybodontoidea indet 1

Cohort Euselachii Hay, 1902

Superfamily Hybodontoidea Owen, 1846

Indet.

2.3.3.4.1 Specimen TMP 83.205.62

Specimen TMP 83.205.62 is a partially preserved post-cranial skeleton (Fig. 2.37). There are two semi-preserved finspines but no basal cartilage, webbing or radials. The largest preserved section includes an incomplete anal and caudal fin.

2.3.3.4.1.1 Caudal Fin

The caudal fin has 26 hypural elements that reduce in size posteriorly ranging is size between 25-10 mm. These hypurals do not appear to extend far enough down into the hypochordal lobe to provide adequate support. It is possible that the first few hypurals were jointed and the lower sections did not survive preservation.

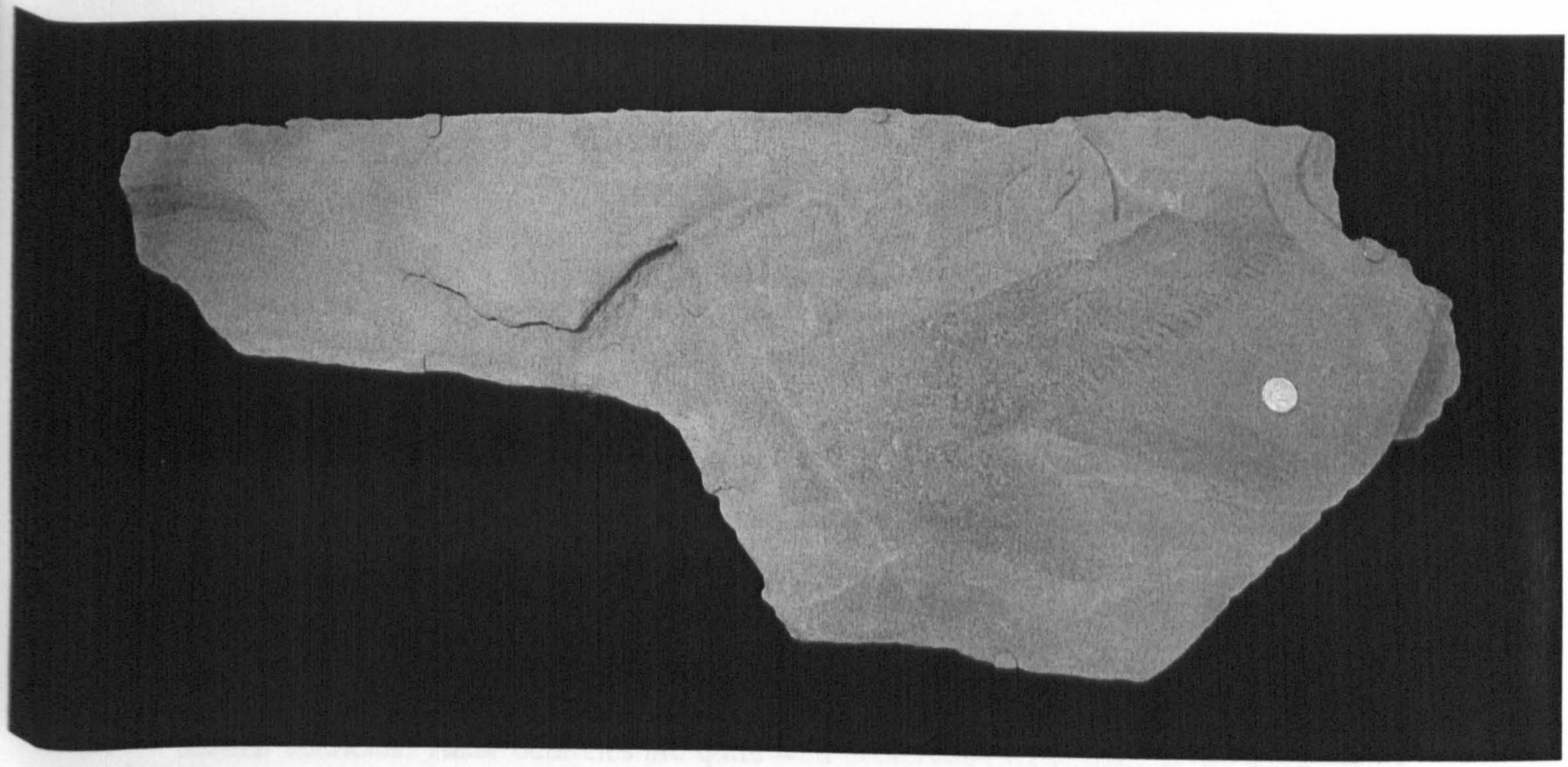


Fig. 2.37. Hybodontoidea indet. TMP 83.205.62

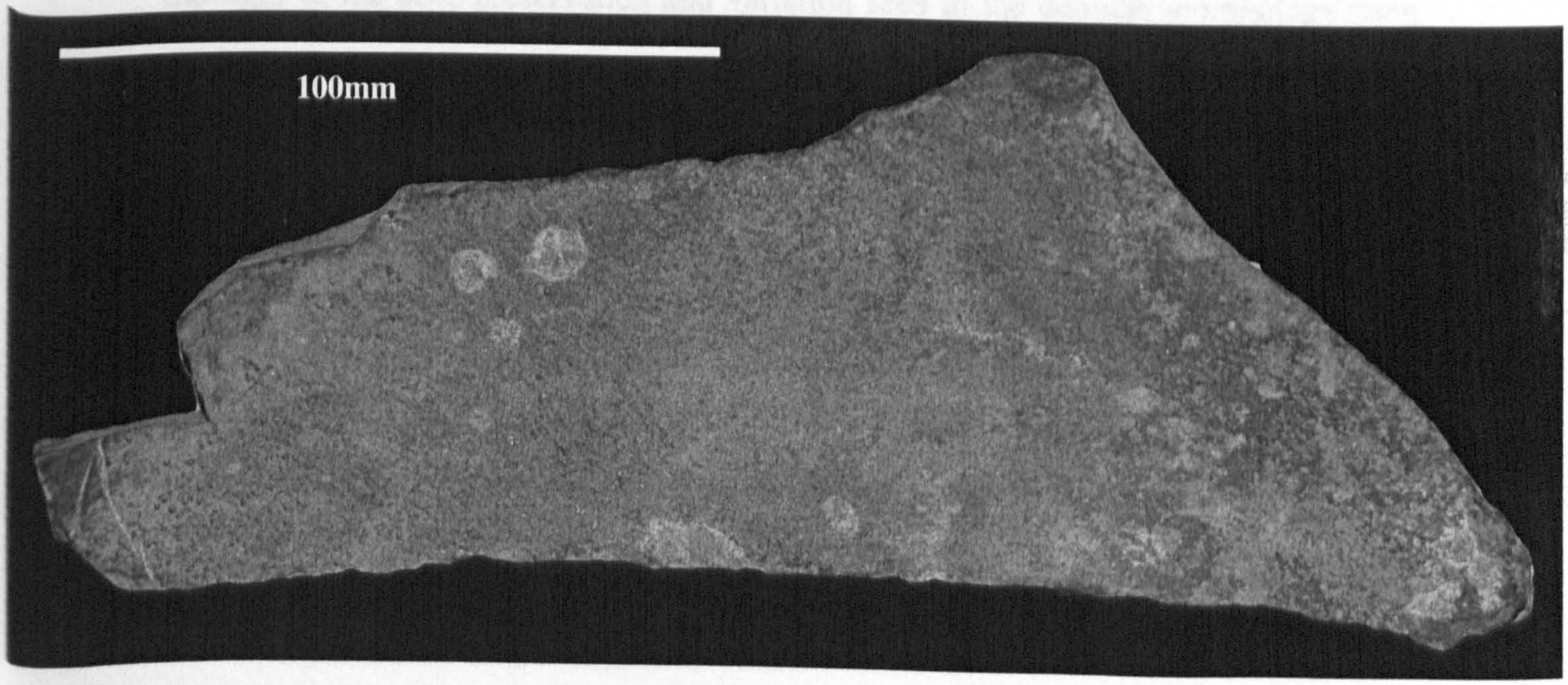


Fig. 2.38. Hybodontoidea indet. sp. no. 17931.

2.3.3.5 Hybodontoidea indet 2

2.3.3.5.1 Specimen UAE 17931

Cohort Euselachii Hay, 1902

Superfamily Hybodontoidea Owen, 1846

Indet.

Another specimen (UAE 17931) that cannot at present be assigned to a genus is a section of preserved skin that is 205 mm in length (Fig. 2.38). The assignment of this specimen to any genus is tenuous as there is no preserved dental of skeletal material only dermal denticles. These denticles are quite well preserved (better than in the body fossils within the collection) and conform to the morphology that Schaeffer and Magnus described as *Palaeobates*. That is to say with a broad base and four extending acuminate projections to the rear and as such are probably from the same genus. It is my opinion that the assignment to *Palaeobates* is difficult to support with only denticles especially in the light of the poor preservation and variation seen in the denticle morphology from most of the Wapiti lake sharks.

2.3.4 Discussion

The generic assignment of many of the specimen in the collection is difficult. Many consist of fragmentary sections of the dorsal column and dorsal fins with no cranial morphology or teeth. The only full-bodied hybodont found from the area was described

by Schaeffer and Magnus (1976) who attributed the specimen (that also lacked teeth) to *Palaeobates* based on dermal denticle morphology which they considered to be similar to *Palaeobates polaris* (Stensiö 1921). Stensiö (1921) describes these denticle as "poorly preserved" and states that a number of ridges extend backwards as "long slender processes" but that the number of these ridges "cannot be stated with certainty". Several of the specimens found from the Wapiti area have denticles with considerable variation . On the same specimen it is possible to find denticles that have no processes to those that have 3-4 posteriorly extending processes. In addition to this I know of no generic classification scheme for hybodonts that would allow generic assignment based on denticles to be convincing. The assignment of the specimen to *Palaeobates* is cast further into doubt when it is seen that while there are several specimens of isolated teeth and a number found in situ, none of these meet the criteria set out by Stensiö to describe *Palaeobates* i.e. "Crown long and narrow, without lateral cones (cusps), but sometimes with principal cone. A longitudinal crista (= longitudinal ridge sensu Reif 1973b, fig 2) is often present but may also be absent. The structure of the crown consists of fine striae sometimes anatomosing to form a network. The crown is covered with a thin layer of enameloid, apart from which it is formed by osteodentine." (quoted from Rieppel 1981). In view of these factors it is assumed in this work that while similarities in dermal denticle morphology may be sufficient to allow the grouping of several specimens from the same locality, it is insufficient to allow the generic assignment of *Palaeobates* with such a small group for comparison.

One specimen (UAE 17932) has the same dorsal finspine and vertebral column morphology as the type specimen of *Wapitiodus* (TMP. 97.74.10) and as such can be considered to be the same species. The other specimens that lack teeth (UAE 46527, 46528, 46529 and 46530) are harder to assign. These bear a similarity to the more robust dorsal finspine morphology found in UAE 46531. UAE 46531 is however much smaller than the four specimens above and while damaged the pectoral fin in UAE 46531 is not very similar to that in UAE46529. It however is possible that UAE46531 is a female and/or a juvenile (though the incompletely preserved nature of the pelvic fin makes this impossible to confirm) which would go some way to explaining the slight size difference in fin morphology. Thus these specimens are tentatively grouped together in the genus *Contrariodus*.

Specimens UAE 46527, 46528 and 46531 have anterior dorsal finpine angles that are similar (53, 40 and 50) and lower than the only TMP.97.74.10 but specimen UAE 46527 has a shallower angle in the posterior dorsal than TMP.97.74.10 and UAE 17932 (61 to 72 and 77) while UAE 46531 has a much higher angle (85). Some spine angles may have been altered during the preservational process, notably the posterior dorsal fin in TMP.97.74.10 in which the basal cartilage appears to have shifted vertically post mortem. As such it is probably not worth using as a diagnostic feature.

Chapter 3.0

3.1 The status of the hybodont genus *Polyacrodus* Jaekel, 1889

3.1.1 Introduction

The state of hybodont systematics has long been in contention and is far from being resolved. This work accepts the hypothesis of Maisey (1982) that hybodonts with orthodont tooth histology and short tumid cusps (such as the Lonchidiidae and the Polyacrodontidae) are the basal taxa while those with osteodont tooth histology (such as the Hybodontidae and the Acrodontidae) represent the more derived families within the Hybodontiformes.

The genus *Polyacrodus* Jaekel, 1889 is currently placed with *Palaeobates* in the family Polyacrodontidae Glikman, 1964 based mainly on dental histology. Cappetta (1987) subsequently included *Lissodus* (with which he synonymised *Lonchidion*) in this family but this has come under criticism (Antunes *et al.* 1990, Rees and Underwood 2002). I consider *Lissodus* and *Lonchidion* to be separate genera and not part of the Polyacrodontidae. Originally assumed to be restricted to the Triassic recent additions to *Polyacrodus* include forms from the Jurassic and Cretaceous. In its current state of revision *Polyacrodus* has no useful diagnosis and cannot be positively identified based on crown morphology (Rees and Underwood 2002). The present paper aims to rectify this shortcoming. To date, 28 species of *Polyacrodus* have been named, as well as a number of records not classified to species level. Of the 28 named species only 13 have diagnoses, the others having been described before the Rules of Zoological Nomenclature made this compulsory or simply not having had one included in the description.

There has been some debate over the diagnosis of *Polyacrodus* (e,g, Antunes *et al.* 1990), with many of the early descriptions and illustrations being ambiguous (Johnson 1981). The original description of *Polyacrodus* by Jaekel (1889) is vague and lists characteristics such as development of the stout, conical central cusp and smaller lateral cusps; short conical morphology of all cusps; short ridges, not covering the sides, running from the occlusal crest and apex of cusps that are less faint and dense that those of *Hybodus*; strong ridges running from apex of central cusp, giving the tooth a pyramidal appearance. Abraded teeth bear a pronounced transverse crest forming a sharp keel under which the sides of the crown decline steeply lacking ridges. This description cannot be used to diagnose *Polyacrodus* as all of these are found in several species of Lonchidiidae. The main distinction between the crown morphology of the Lonchidiidae and *Polyacrodus* was considered to be the presence of a labial peg on the teeth of the former. The size of this peg varies in different species of the Lonchidiidae from "pronounced" to "slight" (Duffin 1985), indicating that it is a continuous, not a discrete character. This would imply that several species assigned to *Polyacrodus* may be Lonchidiidae with labial pegs that are so "slight" as to be unnoticeable. Furthermore when discussing *Polyacrodus*, Rees and Underwood (2002) actually state the possible presence of a labial peg in this genus. Others (J. Kriwet, pers. comm. 2001) have suggested that *Polyacrodus* can be distinguished from *Lissodus* on the basis of having more than one vertical ridge descending from the main cusp. However, this character also appears to be invalid, as several species of *Lissodus* (Duffin 1985, Duffin and Thies 1997) have at least three vertical ridges originating from their main cusp.

In this revision the genus *Polyacrodus* has been split into four genera each comprising between two and ten species with several former *Polyacrodus* species being re-assigned to other genera such as *Lissodus* and *Parvodus*. The diagnoses given for the genera described below are composed of both homoplastic and autapomorphic characters and state the presence or absence of the characters found in all other genera within the family in order to be totally comparable with each other.

3.1.2 Systematic palaeontology

3.1.2.1 *Polyacrodus*

Superfamily Hybodontoidea Owen, 1846

Family Polyacrodontidae Glickman, 1964

Polyacrodus Jaekel, 1889

Type species: *Hybodus polycyphus* Agassiz, 1837. (Middle Triassic of Germany and France).

Neotype: *Polyacrodus polychyphus* (Agassi 1837) Paris Museum of Natural History.

Type stratum: Middle Triassic of Luneville, France

Stratigraphic distribution: Induan to the Albian

Emended diagnosis: Anterior teeth with pyramidal-shaped crown; Main cusp is centrally located and flanked by 1-5 pairs of prominent lateral cusps, cusps are a symmetrical in distribution (i.e. there are the same number of lateral cups on each side of the main cusp); Ornamentation consists of dense and fine to sparse and coarse ridges originating from the

cusps and terminating at the crown/root junction, ridges do bifurcate; Posterior teeth are lower and wider than anteriors; main cusp is centrally located with 1-4 pairs of lateral cusps that are much less prominent than in anterior teeth; symmetry of cusps may vary by one on either side of main cusp; Ornamentation consists of dense and fine to sparse and coarse ridges originating from the cusps and terminating at the crown/root junction, ridges do bifurcate; Root of equal or greater depth than crown; Specialised foramina absent; Labial peg poorly defined or absent; Lingual peg absent; Longitudinal crest absent.

Included species: *Polyacrodus polycyphus* (Agassiz, 1837), from the Middle Triassic of Germany and France, *Polyacrodus twitchetti* nov. gen. from the Lower Triassic of Greenland, *Polyacrodus tregoi* (Rieppel *et al.* 1996) from the Middle Triassic (Anisian) of Nevada, USA. *Polyacrodus delabechei (*Charlesworth, 1839) from the Sinemurian of Lyme Regis, Dorset, England, *Polyacrodus brevicosatus* (Patterson, 1966), from the Wealden of England, *Polyacrodus illingsworthi* (Dixon 1850), from the Wealden of England, the Albian of the Kursk Region, Russia, the Cenonanian of England and the Turonian of Dallas, Texas, USA and *Polyacrodus torosus* (Mertiniene and Nessov 1991), from the Cretaceous (Albian) of Russia.

Discussion: These teeth are typical of the original description of *Polyacrodus* and can be clearly distinguished from *Aconcinnodus* nov. gen. by their symmetrical crown and from *Pseudohybodus* nov. gen. by their pyramidal shaped cusps. The presence of a pyramidal shaped cusp as well as clear lateral cusp distinguishes this genus from *Contrariodus*. The

stratigraphic record of the revised *Polyacrodus* ranges from the Anisian to the Albian with little change in tooth morphology over that time. The cusps vary in labio-lingual thickness between various species of *Polyacrodus. Polyacrodus polycyphus* appears to have the labio-lingually thickest cusps while those of some species (i.e. *P. brevicosatus*) are much thinner. Knots (i.e labial or lingual protrusions that are not confluent with main cusp) are present in *P. torosus* and *P. polycyphus* but absent in all others The presence or absence of knots in certain species is not a synapomorphic character but rather a homoplastic one as they have evolved in several species within several different genera, more than likely with the function of locking teeth rows together. Ornamentation varies between a few coarse ridges in *P. tregoi* to densely packed fine ridges in *P. brevicosatus.* The crown can be either vertical or labially inclined as seen in *P. tregoi.*

The teeth show moderate heterodonty. The main cusp has between one and four lateral cusps on each side but these are not always symmetrically placed. The original description of *Hybodus polycyphus* by Agassiz (1837) indicates four lateral cusps on one side of the main cusp but only three on the other. Like most shark teeth, the anterior teeth are higher with obvious cusps, being less pronounced in the posterior teeth.

Regrettably, the type material of the type species of *Polyacrodus* (*P. polycypus*) was in the Mougeot collection and has been lost, forcing the allocation of a new type specimen. Specimens from the same locality are in the collection of Paris Museum of Natural History but I have yet to receive a specimen number.

3.1.2.2 *Aconcinnodus*

Superfamily Hybodontoidea Owen, 1846

Family Polyacrodontidae Glickman, 1964

Aconcinnodus, n. gen.

Type species: *Polyacrodus pyramidalis* Stensio, 1921 (Upper Triassic of Spitsbergen).

Holotype: P717a

Locus Typicus: Mt. Bertil, Spitzbergen

Strategraphic distribution: Sakmarian to the Rhaetian, Upper Triassic.

Etymology: (Latin) Aconcinnus meaning asymmetrical; odon (Greek) meaning tooth.

Diagnosis: Anterior teeth with long low crown with moderate to high main cusp; Location of main cusp on crown varies and is flanked by 0-4 lateral cusps on either side; cusps are asymmetrically set with one poorly defined cusp on one side and up to 4 more prominent cusps on the other; Ornamentation poorly defined to absent consisting of fine to sparse ridges originating from the cusps and occlusal crest and terminating at the crown/root junction, ridges do not bifurcate; Posterior teeth are lower and wider than anteriors; main cusp is centrally located with no lateral cusps; Ornamentation even less prominent than on anteriors with ridges originating from the cusp and occlusal crest and terminating at the crown/root junction, ridges do not bifurcate; Root less deep than crown; Specialised foramina present; Labial peg poorly defined to absent; Lingual peg absent; Longitudinal crest absent.

Included species: *Polyacrodus witchitaensis* Johnson, 1981 from the Early Permian of Texas, *Polyacrodus pyramidalis* Stensio, 1921, from the Upper Triassic (Rhaetian) of Spitzbergen, *Polyacrodus claveringensis* Stensiö, 1932, from the Lower Triassic of Greenland.

Discussion: These teeth can be distinguished from *Polyacrodus* and *Contrariodus* based on their highly asymmetrical distribution of lateral cusps, and *Pseudohybodus* based on their pyramidal cusps. While there are some symmetrical teeth (i.e. the extreme posteriors) they are still easily distinguishable from *Contrariodus* (no lingual peg) and from *Polyacrodus* and *Pseudohybodus* as anterior teeth in these have at least one pair of lateral cusps (and usually more) while *Aconcinnodus* never has any. If you add this to the other characters that differentiate the genera (i.e. the root size in *Polyacrodus* and the fact that ridges never reach the crow-root junction in *Pseudohybodus*) it is more than enough to support *Aconcinnodus*. *Aconcinnodus* ranges from the Sakmarian to the Rhaetian with very little change in tooth morphology. There is some variation in morphology within *Aconcinnodus*. *A. witchitaensis* (Johnson 1981) has a main cusp with a posteriorly directed apex while the other species in the genus all have vertical main cusps. *A witchitaensis* also has a lingually extended root not present in other *Aconcinnodus* species. *A. pyramidalis* (Stensiö, 1921) is distinct from the other species by having labially curved crowns. The main cusp can be variously located on the crown and is place centrally in *A. witchitaensis* but is located more posteriorly on the crown in *A. pyramidalis* and *A. claveringensis* (Stensiö, 1932). All *Aconcinnodus* species have a single row of specialised foramina.

Where more than just the anterior teeth are found, *Aconcinnodus* does show heterodonty. The posterior teeth have broad and low crowns with no lateral cusps and a poorly defined vertical main cusp. The ornamentation on posterior teeth is far less dense and poorly defined than that on the anterior teeth.

3.1.2.3 *Pseudohybodus*

Superfamily Hybodontoidea Owen, 1846

Family Polyacrodontidae Glickman, 1964

Pseudohybodus, n. gen.

Type species: *Polyacrodus balabansaiensis* (Nessov and Kazynyshkin, 1988)

Type specimen: TSNIGR 1/12397

Locus Typicus: Fergana, Russia

Stratigraphic distribution: Anisian to Maastrichtian, Upper Jurassic.

Etymology: (Greek) Pseudo, meaning false, due to their superficial resemblance to *Hybodus*.

Diagnosis: Anterior teeth with *Hybodus*-like crown shape but with cusps with rounded rather than acuminate tips and orthodont tooth histology; Main cusp is centrally located and flanked by 1-8 pairs of prominent lateral cusps, cusps are symmetrical in distribution; Ornamentation consisting of ridges that are low in density but prominent and sharp

originating from the cusp apices and terminating before the crown/root junction, ridges do bifurcate; Posterior teeth are lower and wider with posteriorly recurved cusps, main cusp is asymmetrically located on crown with 1-3 pairs of lateral cusps that are less prominent than those on anterior teeth, symmetry of cusps may vary by one on either side of main cusp; Ornamentation is less prominent than on anterior teeth with ridges originating from the cusps and terminating before the crown/root junction, ridges do bifurcate; Root less deep than crown; Single row of specialised foramina present; Labial peg poorly defined to absent; Lingual peg absent; Longitudinal crest absent.

Included species: *Polyacrodus* sp. A, Rieppel *et al.* 1996, from the Middle Triassic (Anisian) of Nevada, USA. *Polyacrodus keuperianus* (Winkler, 1880), from the Middle Triassic (Muschelkalk) of Germany. *Polyacrodus krafti* (Seilacher, 1943), from the Middle Triassic (Muschelkalk) of Germany. *Polyacrodus cloacinus* (Quenstedt, 1858), from the Rhaetian of Barnstone, Nottinghamshire, England. *Polyacrodus raricostatus* (Agassiz, 1843), from the Sinemurian of Lyme Regis, England. *Polyacrodus obtusus* (Agassiz, 1837), from the Bathonian of Caen, Upper Kimmeridgian of Normandy and Lower Tithonian of La Rochelle France. *Polyacrodus parvidens* (Woodward 1916), from the Tithonian to Valangilian of Dorset, England. *Polyacrodus siversoni* Rees, 1999, from the Early Campanian of the Kristianstad Basin, Sweden. *Polyacrodus balabansaiensis* Nessov and Kazynyshkin, 1988, from the Late Jurassic of northern Fergana, Russia. *Polyacrodus prodigialis* Nessov and Kazynyshkin, 1988, from the Late Jurassic of northern Fergana, Russia.

Discussion:

Teeth of *Pseudohybodus* can be distinguished from those of other Polyacrodontidae by their higher, posteriorly recurved cusps and the lower part of the labial side of the tooth, which is free of ornamentation. These teeth bear a slight resemblance to *Hybodus* but can be clearly distinguished from these on the basis of their shorter, squatter and more rounded cusps and their orthodont tooth histology. Several species of *Pseudohybodus* including *P. raricostatus* and *P. obtusus* have been previously assigned to *Hybodus* but, due to their dental histology do not belong within this genus (Candoni, 1995) necessitating their allocation to *Pseudohybodus*. The stratigraphic record of *Pseudohybodus* ranges from the Anisian to the Maastrichtian. Ornamentation in *Pseudohybodus* varies slightly but the ridges are generally low in density but prominent and sharp. Some species such as *P. keuperianus* have ridges that are strait, sharp, few in number and often bifurcating. The ridges in *P. parvidens* are coarse and do not reach the apex of the cusps. *P. balabanensis* has ridges that are narrow and sparsely distributed. Labial knots are variously present. *P. cloacinus* has knots beneath or diagonally beneath the cusps while *P. raricosatus* has them at the base of ridges descending from the cusps. *P. silversoni* has knots on the first and second pair of later cusps. The number of lateral cusps in *Pseudohybodus* varies from one to three pairs in most species and from four to eight in *P. parvidens*. Labial pegs (i.e protrusions that are confluent with the main cusp) are present in *P. krafti, P. silversoni, P. parvidens* and *P. raricostatus*. The main cusp in *P. cloacinus* is bent lingually giving the teeth the appearance of being labially convex. *P. parvidens* has a labial longitudinal keel while a lingual shelf is present on the crest of the

lingual crown shoulder in *P. raricostatus*. The roots in *Pseudohybodus* are generally vertical but in *P. parvidens* they are inclined lingually with a flat basal face. There is a moderate heterodonty in *Pseudohybodus* with posterior teeth having lower cusps and often having a slightly asymmetrical distribution of lateral cusps but not nearly as obvious as in *Aconcinnodus*.

3.1.2.4 *Contrariodus*

Superfamily Hybodontoidea Owen, 1846

Family Polyacrodontidae Glickman, 1964

Contrariodus n. gen.

Type species: *Polyacrodus contrarius* Johns *et al.*, 1997 from the Carnian of Canada

Holotype: GSC 105093

Locus Typicus: Peace River Formation, Canada

Stratigraphic distribution: Anisian to the Rhaetian.

Etymology: Named for type species.

Diagnosis: Anterior teeth with low, triangular but not pyramidal shaped crown; Main cusp is centrally located and flanked by 0-1 poorly defined pair of lateral cusps, cusps are symmetrical in distribution; Ornamentation made of very sparse ridges originating from the occlusal crest and terminating at the crown/root junction, ridges do not bifurcate; Posterior teeth are lower and wider than anterior teeth; main cusp is centrally located with no lateral cusps; Ornamentation is even less prominent than on anterior teeth with ridges

originating from the cusps and terminating at the crown/root junction, ridges may bifurcate; Root less deep than crown; Specialised foramina absent; Labial peg poorly defined or absent; Lingual peg prominent; Longitudinal crest present.

Included species: *Polyacrodus contrarius* Johns *et al.*, 1997, from the Ladinian and Carnian of Canada, *Polyacrodus bucheri* Cuny *et al.*, 2001, from the Anisian of Nevada, USA, Polyacrodus holwellensis Duffin 1998 from the Rhaetian of England

Discussion:

Contrariodus can be distinguished from *Polyacrodus, Aconcinnodus,* and *Pseudohybodus* by its triangular (but not pyramidal) crown, its highly reduced to absent lateral cusps and a distinct lingual peg. The stratigraphic record of *Contrariodus* ranges from the Anisian to the Carnian. The differences between three species are minimal. *C. contrarius* has labial and lingual shoulder protrusions as well as a lingual peg. *C. contrarius* also has labial and lingual knots that are lacking on *C. bucheri and C. holwellensis. C. contrarius* also has more pronounce ornamentation than the other two species. *C. holwellensis* is known only from poorly preserved posterior teeth and as such is only preliminarily assigned to *Contrariodus* pending the discovery of better material.

3.1.3 Summary

The previously described *Polyacrodus* species above fall into one of six categories. Some (*P.* sp. B, *P. zideki, P. lapolamensis* and *P. richei)* meet Rees and

Underwood's (2002) definition of *Lissodus*. *P. gramanni*, despite the lack of a well developed labial peg, is placed in *Parvodus* (Rees and Underwood 2002). Of the others (*P. polycyphus, P. tregoi*, P. *delabechei, P. rugianus, P. brevicostatus, P. illingsworthi* and *P. torosus)* fall in a single genus which retains the name *Polyacrodus*. *P. wichitaensis, P. pyramidalis* and *P. claveringensis* are assigned to a second genus given the name *Aconcinnodus*. sp A. *P. krafti*, P. *keuperianus, P. cloacinus, P. raricosatus, P. obtusus, P. silversoni, P. parvidens, P. balabanensis* and *P. prodigialis* are grouped together and named *Pseudohybodus* due the their *Hybodus*-like crown shape but with rounded rather than acuminate cusps. Finally, *P. contrarius* and *P. bucheri* are grouped together and assigned to *Contrariodus*.

While *Polyacrodus, Aconcinnodus, Pseudohybodus* and *Contrariodus* are all assigned to the Polyacrodontidae based on orthodont tooth histology and a lack of a well defined labial peg no diagnosis is included for the family in this work. All species currently assigned to the above genera are based on isolated teeth with no more complete specimens on which to base any systematic conclusions. These teeth have certain characteristics in common, among them the already mentioned orthodont tooth histology, the lack of a well-developed labial peg and a low broad crown suited to a generalised feeding strategy (i.e. feeding on a wide variety of prey including hard and soft bodied prey). All of the characters shared by these genera are, however, either undiagnostic or plesiomorphic and hence are not sufficient to constitute a diagnosis. In this work the family Polyacrodontidae is considered to be a plesion (i.e. a stem group in which

monophyly cannot be demonstrated due to a lack of derived characters) pending the discovery of more detailed and diagnostic material.

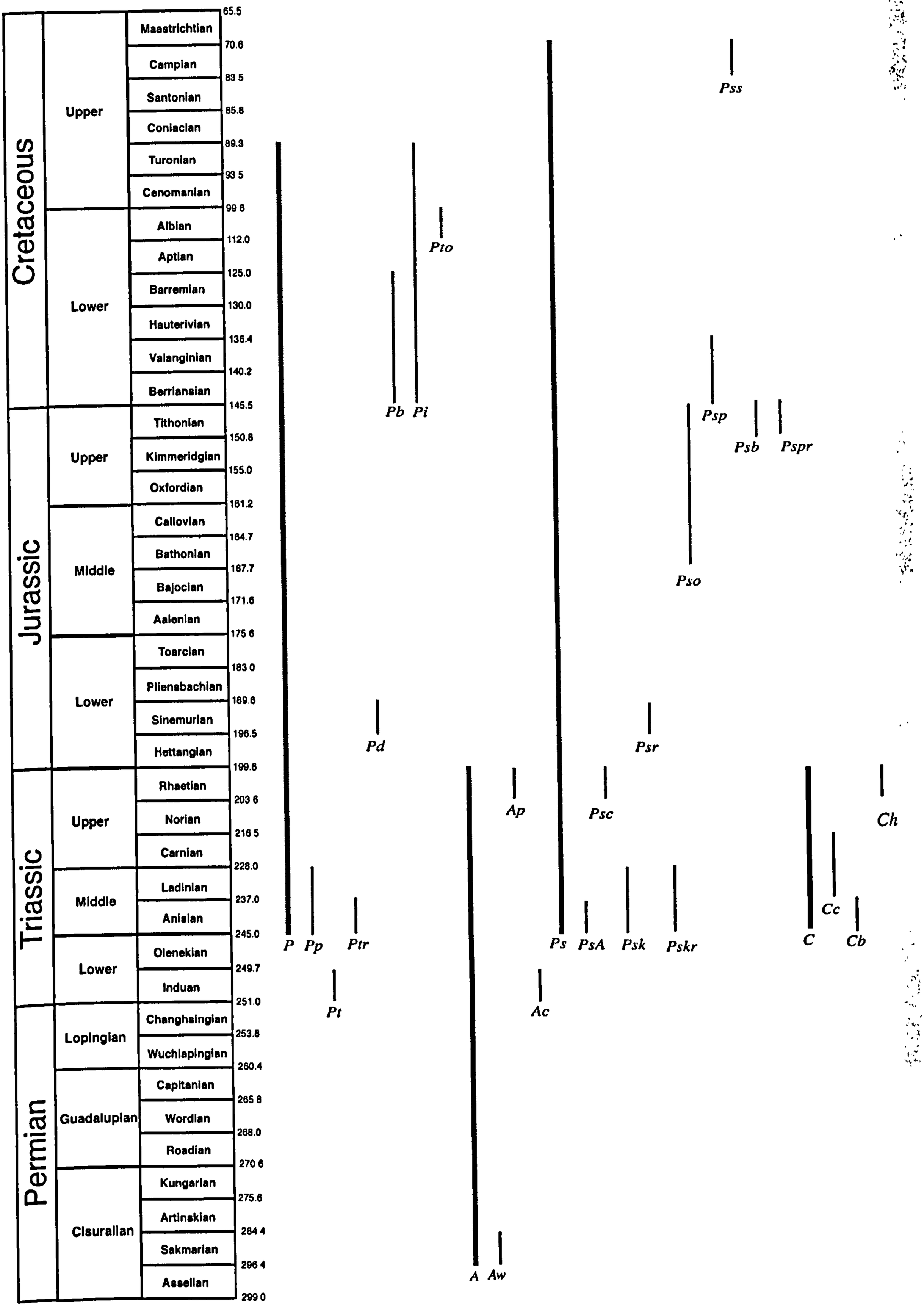


Fig 3.1: Range chart of Polyacrodontid genera and species. *P = Polyacrodus, Pp = P. polychyphus, Pt = P. twitchetti, Ptr = P. tregoi, Pd = P. delabechei, Pb = P. brevicostatus, Pi = P. illingsworthi, Pto = P. torosus, A = Aconcinnodus, Aw = A.witchitaensis, Ap = A. pyramidalis, Ac = A. claveringensis, Ps = Pseudohybodus, PsA = P. sp A, PSc = P.cloacinus, Psk = P. keuperianus,, Psr P. raricostatus, Pskr = P.krafti, Pso = P. obtusus, Psp = P. parvidens Pss = P. silversoni, Psb = P. balabansaiensis, Pspr = P. podigialis, C = Contrariodus, Cc = C. contrarius, Cb = C bucheri, Ch = C. holwellensis.*

Chapter 3.2 The State of Lower Triassic Hybodont Systematics

3.2.1 Introduction

The aim of this section is to give an overview of the current state of Lower Triassic hybodont systematics in order to be able to get a more accurate view of the change in diversity over the P-Tr boundary (Chapter 5.1). There are several genera of Mesozoic hybodont that either lack diagnoses or the diagnosis of which are unclear. It is beyond the scope of this work to attempt to resolve the systematics of several of these genera, notably *Hybodus* that comprises more species than any other hybodont genus but lacks any clear diagnosis. Likewise there are several genera of Mesozoic hybodont that are not found in the Lower Triassic and it is beyond the scope of this work to resolve these. Of the genera that will be considered those that have diagnoses (either taken from the literature or revised elsewhere in this work) are *Polyacrodus, Aconcinnodus, Lissodus* and *Wapitiodus,* while those that have no valid diagnoses are described based on the initial descriptions with additional characters provided by subsequent literature are *Acrodus, Palaeobates* and *Hybodus.* Diagnoses and descriptions referenced from other works have been left in their original form while original and translated diagnosis and descriptions all use a standardised terminology, i.e main cusp, lateral cusps, ridges (rather than striations), occlusal crest and labial peg.

3.2.2 Hybodonts in the Permian

There are several genera of hybodonts in the Permian. Branson (1933) described three genera from the Lower Permian of the USA which he assigned to *Dolohonodos, Hamatus* and *Ancisrtiodus.* He later synonymised these with *Arctacanthus* (Nielson 1932) found in the Upper Permian of Greenland (Branson 1934) . All material found consisted of isolated cephalic spines. Four other genera of hybodont were found in the Permian and all survived the end Permian event. *Aconcinnodus* was found in the Lower Permian of the USA (Johnson 1981) as was *Acrodus* and *Lissodus*. *Lissodus* was also discovered in the Upper Triassic of Russia (Ivanov 1999). Finally *Hybodus* was also located in the Lower Permian of the USA (Simpson 1974).

3.2.3 Lower Triassic Hybodonts

3.2.3.1 Polyacrodontidae Glückman, 1964

3.2.3.1.1 *Polyacrodus* Glückman, 1964

Polyacrodus has been dealt with in detail elsewhere in this work (Chapter 3.1) and as such I will not go into excessive detail here. The genus *Polyacrodus* has been in a near constant state of contention since it was first erected by Glückman in 1964. Below is an emended diagnosis based on an examination of all species currently assigned to *Polyacrodus*, many of which have since been placed in other genera (Chapter 3.1).

Emended diagnosis: Anterior teeth with pyramidal-shaped crown; main cusp centrally located and flanked by 1-5 pairs of prominent lateral cusps, cusps symmetrical in distribution; ornamentation consists of dense and fine to sparse and coarse ridges originating from the cusps and terminating at the crown/root junction, ridges bifurcating; posterior teeth lower and wider than anteriors; main cusp centrally located with 1-4 pairs of lateral cusps that are much less prominent than in anterior teeth; symmetry of lateral cusps may vary by one on either side of main cusp; ornamentation consists of dense and fine to sparse and coarse ridges originating from cusps and terminating at crown/root junction, ridges bifurcating; root of equal or greater depth than crown; specialised foramina absent; labial peg poorly defined or absent.

3.2.3.1.2 *Aconcinnodus* n. gen.

Aconcinnodus is one of the new genera erected to accommodate some of the species previously attributed to *Polyacrodus*. Like the genus *Polyacrodus, Aconcinnodus* is dealt with in chapter 3.1 and as such only the diagnosis is included below.

Diagnosis: Symphyseal teeth with high pyramidal central cusp with 0-1 pair of very poorly defined to absent lateral cusps; anterior teeth with long, low crown with moderate to high main cusp; location of main cusp on crown varies, flanked by 0-4 lateral cusps on either side; lateral cusps asymmetrically set with one poorly defined to absent on the mesial side and up to four more prominent on distal side; ornamentation poorly defined to

absent consisting of fine to sparse ridges originating from the cusps and occlusal crest and terminating at the crown/root junction, ridges not bifurcating; Posterior teeth lower and mesio-distally wider than anteriors; main cusp centrally located with no lateral cusps; ornamentation even less prominent than on anteriors with ridges originating from cusps and occlusal crest and terminating at the crown/root junction, ridges not bifurcating; root less deep than crown; no specialised foramina; labial peg poorly defined to absent; lingual peg absent.

3.2.3.1.3 *Palaeobates* Meyer, 1847

Originally described as *Psammodus* and then *Strophodus* (Agassiz 1837) the genus *Palaeobates* was erected by Meyer in 1847. Meyer gave a brief and largely undiagnostic description and stated that he considered the teeth of the type species to be most closely related to *Myliobatis* and *Zygobatis* (i.e. rays). *Palaeobates* was subsequently placed in a number of groups by various workers before being placed in the Hybodontiformes. Stensiö (1921) produced a more diagnostic description of *Palaeobates* (included below) later referred to by Rieppel (1981) that included the following characters: crown long and narrow without lateral cusps but occasionally including a main cusp.; longitudinal ridge often present; ornamentation consisting of fine ridges occasionally anatomising to form a network; Crown covered by a thin layer of enameloid but otherwise composed entirely of orthodentine.

Description (Stensiö 1921): Mandible short and high with comparatively few, probably only five or six, transversal rows of teeth; possibly an unpaired symphyseal row is also present. The third and fourth transverse rows, counting from behind, each consist of long, large teeth, the rows that follow anteriorly and posteriorly consist of smaller teeth , the most posterior row having even very small teeth. The anterior teeth have a more strongly arched crown than those following posteriorly. The dentition in the palatoquadrate is not known in detail, but it possibly differs somewhat from that in the lower jaw. All the teeth, both in the palatoquadrate and the mandible, have a flattened, long and narrow crown without lateral cones (lateral cusps) but sometimes with a principle cone (main cusp). A longitudinal crista (occlusal crest) is often present, but may also be absent. The sculpture of the crown consists of fine, very much ramified striae (ridges), in certain species anatomosed with each other and forming a network. The crown has a rather thin layer of enamel, aside from which it is entirely formed of ortho-dentine; the root consists of trabecular-dentine. There is often the remains of a pulp cavity between the root and the crown.

3.2.3.1.4 *Wapitiodus* n. gen.

Wapitiodus is a new genus based on previously undescribed material from the Lower Triassic of the Wapiti Lake area of British Columbia. The material has been described in full in chapter 2.3.3.1 and as such only the diagnosis is included below.

Diagnosis: Body short and robust, dorsal finspines comparatively gracile; anterior teeth with high acuminate main cusp and with concave crown base; main cusp centrally located with no lateral cusp; ornamentation consists of dense and fine ridges originating from crown-root junction and ascending the crown but not reaching the occlusal crest; posterior teeth lower and wider than anteriors; main cusp very reduced or absent with no lateral cusps; ornamentation consists of sparse and coarse ridges originating from cusps and terminating at crown/root junction, ridges bifurcating; root of equal or greater depth than crown labial peg poorly defined or absent; lingual peg absent.

3.2.3.2 Lonchidiidae Herman, 1977

3.2.3.2.1 *Lissodus* Brough, 1935

Lissodus was erected by Brough in 1935 and is known from full body fossils as well as isolated teeth. In 1985 Duffin proposed that *Lissodus* and *Lonchidion* be synonymised, based largely on the presence of a labial peg confluent with the main cusp, a contention later accepted by Cappetta (1987). This character, the grouping of these two genera, as well as several others were later criticized by Antunes *et al.* (1990) decause that not all of the similarities are confined to the genera in question. A recent review of *Lissodus* has been done by Rees and Underwood (2002). In this work they distinguish between *Lissodus* and *Lonchidion* though both were put in the family Lonchidiidae. The most obvious character separating *Lissodus* and *Lonchidion* from other lonchidiidae genera is a well-developed crown shoulder, particularly obvious on the lingual side.

According to Rees and Underwood the family Lonchidiidae also contains the genus *Hylaeobatis* Woodward, 1916 as well as two newly created genera *Vectiselachos* and *Parvodus,* though none are present in the Permian or Triassic. The current most useful diagnosis of *Lissodus*, included below, is taken from Rees and Underwood (2002).

Diagnosis (Rees and Underwood 2002): Jaws deep, lower jaw tapering anteriorly; anterior teeth with a moderately to well developed central cusp, occlusal crest and labial protuberance; occlusal face of labial protuberance (labial peg) sloping gently towards crown base; crown shape almost triangular in occlusal view; lateral teeth lower, larger, more mesio-distally expanded; occlusal crest and labial protuberance (labial peg) poorly developed; root lingually inclined, lower than crown, not as voluminous; single strictly horizontal row of small circular foramina near crown root junction; basal plate of cephalic spines 'T-shaped' with terminally expanded lobes.

3.2.3.2 Acrodontidae Casier, 1959

3.2.3.2.1 *Acrodus* Agassiz, 1837

Acrodus was originally described by Agassiz in 1837 based on isolated teeth. As yet there is no clear diagnosis for the genus with the original description (translated from the French below) being most commonly used, despite a preserved skull being found (Thomson 1982). *Acrodus* has been placed in the Hybodontiformes based on finspine and

tooth histology. The finspine in *Acrodus* is not significantly different from that in *Hybodus* or *Palaeobates* in either external morphology or histology (Rieppel 1981) and the tooth histology of *Acrodus* is identical to that of *Hybodus* (Rieppel 1981). The only difference used to distinguish *Acrodus* from *Hybodus* is tooth morphology, which is low and blunt (durophagous) in *Acrodus* while tall and acuminate (piscivorous) in *Hybodus*. This has led many workers (Maisey 1978, Rieppel 1981) to question the validity of the genus stating that this difference could be due to dietary specialisation within a single genus.

Original Description (translated from Agassiz 1837): As in cerastodonts the enamelled part of the teeth is carried on a bone with a granular structure in the shape of a parallelogram inclined on its internal side. I have not been able to verify this character on all species within the genus but it is so striking in those that I have seen that it is undoubtedly generic. The crown bulges in the centre, is rounded on the sides and is reduced at the two ends. The entire enamelled face is ornamented by transverse ridges that give each tooth its own particular aspect. These ridges ramify uniformly on the entire surface of the crown, always originating from a occlusal crest that itself results from the joining of medial ridges, they extend towards the ends starting from a single central point in the case of the anterior teeth or from several points on the longitudinal crest, forming an acute angle with it, in the posterior teeth.

3.2.3.3 Hybodontidae Owen, 1846

3.2.3.3.1 *Hybodus* Agassiz, 1837

Originally described by Agassiz in 1837 *Hybodus* remains a poorly defined and enigmatic genus. The original description (translated below from the original French) lists characters such as: Anterior teeth with a main cusp that is lengthened, pointed and flanked on both sides by a number of lateral cusps that reduce in size from the centre outwards. The number of lateral cusps is not always equal on both sides of the crown. I have thus far not seen more than four on each side. The labial face of the main cusp is flatter than the lingual face and the ends are extended, this never renders the labial surface completely flat or even concave as in some tertiary and modern sharks. The entire surface of the tooth is covered by vertical ridges. Ridges can extend to the tip of the main cusp especially when this is not too high but often they terminate half way to two thirds up the cusp.

Others have characterised *Hybodus* teeth as having high pointed crowns. Woodward described *Hybodus* as having "Teeth conical or cuspidate, the crown more or less striated, with one principal elevation, and one or more lateral prominences on either side diminishing from the centre" (Woodward 1912-16), while Maisey characterised them as having "multicuspid acuminate teeth" (Maisey 1987). Rees and Underwood (2002) described *Hybodus* as "encapsulating the tooth morphologies of *H. reticulatus*, *H. hauffianus*, *H. delabechi*, and *H. medius*" , but stated that comparisons based on skeletal characters where more complex and needed "quite a lot of work". All species listed by

Rees and Underwood possess the conical and acuminate cusp, flanked by lateral cusplets that reduce in size originally listed as the main character by Agassiz in 1837. As no valid diagnosis exists and no skeletal material from *Hybodus* has been found in the lower Triassic for the purpose of this work these characters will be used to define the genus.

Original Description (translated from Agassiz 1837): Teeth are generally not too massive and are characterised by a main cusp that is lengthened and pointed. This cusp that in many species is as high as the crown in long is flanked on both sides by a number of lateral cusps that reduce in size from the centre outwards in such a way that the one immediately next to the main cusp is the largest, and the one furthest from the main cusp is the smallest. The number of lateral cusplets is not always equal on both sides of the crown. I have thus far not seen more than four on each side and often there are only two. The teeth that are completely devoid of lateral cusplets do not appear normal and are probably poorly preserved. The labial face of the main cusp is flatter than the lingual face and the ends are extended; this never renders the labial surface completely flat or even concave as in some tertiary and modern sharks.

Differences between anterior and posterior teeth are similar to those seen in modern sharks but are less pronounced here. The posterior teeth have a stunted development and the main cusp instead of being extended and pointy like in anterior teeth remains low, button like and more or less extended. The main morphology is the same and it is not much more difficult to recognise posteriors as it is anteriors.

Another character of *Hybodus* is the structure of the enamel. The entire surface of the tooth is covered by vertical ridges (longitudinal in the case of the cusps), that are

more or less fat, depending on species, but generally very distinct. There are several species in which these ridges go up to the point of the main cusp especially when this is not too high but often they terminate half way to two thirds up the cusp but they are always accentuated and when the base is very narrow these form small pads as is the case in *H. reticulatus*. The root of the tooth is fat and its shape resembles that of cerastodonts more than that of modern sharks. Externally it is not that different from the enamelled portion of the tooth in that it is ordinarily the same colour and just as smooth. It is only when examining a cross section that we see the reticulated structure that characterises it. The root is generally parallel to the base of the crown, or rather it is the base of the crown that follows the contours of the root in such a way that if the lower face of the root is horizontal or lightly concave the base of the crown will be also.

Chapter 4

4.0 Local faunal changes over the P-Tr boundary

4.1 Stratigraphy

The times from which fossils will be considered within this study stretch from the Upper Permian to the Lower Triassic, i.e. the Roadian to the Olenekian. The exact stages from which the specimens have been found are outlined below. The relevant information has been grouped geographically rather than in stratigraphic order for ease of understanding.

The Lower Triassic specimens from the United States come from two different formations. The *Orctacanthus* specimens from North Central Texas come from the Arroyo Formation, dated as Lower Leonardian (Sullivan and Reisz 1999), corresponding to the Artinskian to the Roadian. The *Helicoprion* specimens from the United States come from the Phosphoria Formation, dated as Roadian-Wordian (Wardlaw and Collinson 1984)

All of the specimens from the Lower Triassic of Canada come from the Sulphur Mountain Formation, Vega Phroso Siltstone Member of the Wapiti Lake area of British Columbia. There has been some speculation about the exact dating of this formation but the generally accepted view is that the Vega Phroso Member is Olenekian in origin (Orchard and Tozer 1997).

There is only one shark specimen from the Lower Triassic of Brazil and the dating of this specimen is very vague. The specimen comes from the Rio do Rasto Formation, which has been described only as Lower Triassic (Richter and Langer 1997).

Sharks have been found from both the Upper Permian and Lower Triassic of Greenland. The Upper Permian edestid sharks from Greenland come from the Kap Stosch Permian Fish Zone associated with the *Posidonomya* beds, dated as Wuchiapingian (Stemmerik *et al.* 2001). The *Arctacanthus* specimens from Greenland also come from the Kap Stosch region (section F 12 m above the sea) and are also dated as Wuchiapingian (Nielsen 1932). The Lower Triassic shark specimens come from two localities. The first is described as Triassic fish zone II by Nielsen (1952) and is associated with *Otoceras* ammonoid species. The presence of *Otoceras* is characteristic of the base of the Triassic (Permophiles 1980). The second locality is "section X" of the Wordie Creek Formation within the *Hindeodus parvus* conodont zone, the basal conodont zone of the Lower Triassic (Yin 1994).

The Lower Triassic specimens from Spitzbergen fall into three groups. The first group consists of those originally described by Stensiö (1921) from what he called the "Lower Triassic fish zone", later identified as the Sticky Keep Formation (Birkenmajer and Jerzmañska 1979) and dated as Upper Olenekian. The second group is a subset of the original group that were also subsequently identified and described from the Brevassfjellet *Myalina* Beds (Birkenmajer and Jerzmañska 1979), which has been dated as Lower Olenekian. Finally there is *Lissodus angulatus* that Stensiö (1921) describes as coming from "fish horizon 1" and which is associated with *Otoceras* ammonoids, indicating an Induan age.

The *Wodnika* species found from the Upper Permian of Germany was described as coming from the Kupferschiefer (Holzaphel *et al.* 1984). The German Kupferschiefer is located between the Roliegendes and Zechsteinkalk and is dated as Roadian

(Piestrzyñski *et al.* 2000). The *Palaeobates* specimens from the Lower Triassic of Germany are described as Middle Bunter. The Bunter spans the entire Lower Triassic (Harland *et al.* 1982) suggesting an Olenekian age for these specimens.

The *Synechodus* tooth found from the Lower Triassic of Turkey was associated with the conodont *Neospathodus cristagalli* and so was identified as coming from the *cristigall*i one (Thies 1982), which is dated as Lower Olenekian (Sweet 1988).

The *Lissodus* specimens from the Lower Triassic of Angola come from the Cassange series. The exact dating of the series is not entirely clear but the accepted view is that the "beds with fishes" can be dated as Lower Olenekian (Antunes *et al.* 1990, Duffin 2001).

The specimens from the Lower Triassic of Madagascar come from the fish beds of the Middle Sakamena Group which Beltan (1996) dated as Lower Olenekian.

The *Lissodus* specimens from the Lower Triassic of South Africa come from the Lower *Cynognathus* Zone, Upper Beaufort Series (Karroo system). This is aged as Lower Triassic, although Duffin (2001) states that the specimens can be more accurately dated as Lower Olenekian.

Russia has also yielded specimens from both the Upper Permian and Lower Triassic. All of the specimens from the Upper Permian of Russia come from the continental freshwater beds of the East European Platform. The fish bearing horizons are dated as Wuchiapingian to Changhsingian (Tverdokhlebov *et al.* 2005). The Lower Triassic specimens from Russia come from the Petropavlovsk Formation and Yarenskiy Horizon, both dated as Lower Olenekian (Minikh 1985).

The *Triodus* specimens from the Lower Triassic of India come from the *Otoceras* zone. As previously stated, the presence of these ammonoids is indicative of the base of the Induan. The *Acrodus* specimen from the Lower Triassic of India comes from the Khreuh and Guryul Ravine sections, both dated as Lower Induan (Permophiles 1980 1(4))

The *Helicampodus* specimen from Pakistan comes from the Chhidru Formation that has been dated as Wuchiapingian (Shen *et al.* 2003)

The *Helicoprion* specimen from the Upper Permian of Japan comes from the Dalong Formation (Lei 1983), which is dated as Changhsingian (Shao *et al.* 2003). The Lower Triassic specimens from China are described as coming from the Loulou Formation, which spans the entire Lower Triassic but the sharks have been more accurately dated as Lower Olenekian (Wang *et al.* 2001).

A single tooth of a hexanchoid was found from the Upper Permian Kashiwardiara Formation of Japan. This corresponds to the Capitanian (Goto *et al.* 1996). The *Helicoprion* specimen from the Upper Permian of Japan comes from the Konokura Formation while the *Helicampodus* specimen comes from the Toyoma Formation. Both are dated as Wuchiapingian. The final Upper Permian shark specimen from Japan comes from the Senmatsu Formation, which is dated as Changhsingian (Goto *et al.* 1996). The only Lower Triassic shark specimen from Japan is described as coming from the Taho Formation, which spans the entire Lower Triassic (Goto *et al.* 1996), and no more accurate age is given for the specimens.

4.2 USA

4.2.1 Upper Permian

Orthacanthus Agassiz, 1843

The *Orthacanthus* specimens from the USA all come from North Central Texas, from a number of localities in either the Arroyo or Belles Plains Formations (Hotton 1952). These correspond to the period between the Sakmarian and Ufimian. The finds consist of fairly well preserved sets of jaws and hyoid arches, and are from two different species; *O. texensis,* of which there are four specimens, and *O. platypternus* of which there are two.

One of the characters that has traditionally been used to define the genus *Orthacanthus* is the presence of serrations on the main cusp (Hampe 1988, 1993, 1995, Schneider 1988, 1996). If this character is accepted then the apparent lack of serrations on the teeth of *O. platypternus* would exclude it from the genus, with some referring the species to *Xenacanthus* (Schneider and Zajic 1994). There are however other factors to consider when placing *O. platypternus*. On the basis of Johnson (1979, 1999) and the presence of "incipient serrations" (Zidek 1993) *O. platypternus* cannot be placed within *Xenacanthus*. In addition to this the spines associated with *O. platypternus* teeth meet the criteria for *Orthacanthus* laid out by Zidek (1993) and Soler-Gijón (1997). For this reason the preliminary diagnosis for *Orthacanthus* given in Johnson (1999) which states that the teeth "may or may not be serrated" is accepted.

O. texensis Cope, 1884

Diagnosis

Base with labio-lingual dimension usually greater than anteromedial-posterolateral dimension; basal tubercule usually restricted to the labial portion of the tooth base, only occasionally extended to center; labial margin between basal tubercule and oral surface of base is thicker between main cusps than at anteromedial-posterolateral margins of the cusps. Major principal cusp more divergent and often more coarsely serrated than the minor principal cusp. One or more intermediate cusp usually present. (from Johnson 1999)

Type specimen: AMNH 7117

Type Stratum: Wichita Group (Artinskian-Roadian), Texas, USA

O. platypternus Cope,1884

Diagnosis

Tooth base with labio-lingual dimension less than anteromedial-posterolateral dimension; basal tubercule often flat, extending to centre of base; labial margin between basal tubercule and oral surface of base between main cusp is as thin as the base of the anteromedial-posterolateral margins of the main cusp. Major principal cusp generally straight or leaning slightly towards minor cusp, which diverges posteriorly in lateral

teeth; cusps always lack serrations. Intermediate cusp rarely absent and almost always single. (from Johnson 1999)

Type specimen : AMNH 7243

Type Stratum: Wichita Group (Artinskian-Roadian), Texas, USA

Helicoprion Karpinsky, 1899

All the *Helicoprion* specimens from the USA come from two localities in south east Idaho from beds in the Phosphoria Formation (Bendix-Almgreen 1966). This corresponds to the period between the Wordian and the Capitanian. There are ten specimens of *Helicoprion* assigned to two species (*H. ferrieri, H. ergassaminon).* In addition to these two species a number of specimens have been assigned to *H.* cf. *ferrieri* and *H.* sp. The finds consist mainly of symphyseal tooth whorls but one specimen of *H. ferrieri* has a partially preserved neurocranium.

H. ferrieri Hay, 1907

Diagnosis

The neurocranium consists of cartilage with an inner and an outer layer of prismatic calcifications lining the cranial cavity and the outer surface. A rostrum consisting of at least one rod of cartilage situated ventrally in the median line is present. The palatoquadrates are independent elements attached to the neurocranium, possibly in

an amphistylic or hyostylic manner. The lower jaw, consisting of calcified cartilage, possesses a long, high but narrow symphyseal portion, formed by a spiral-coiled symphyseal crest lying between two halves of the Meckel's cartilage which terminates rostrally to the symphysis. Between the branches of the jaw and inside the symphyseal crest, there is a cavity, the symphyseal cavity, which contains the older parts of the symphyseal tooth-spiral. The dentition comprises a strongly developed symphyseal tooth spiral situated in the lower jaw and a few rather small crushing teeth in rows on the anterior part of the upper jaw. The symphyseal tooth spiral is formed in its oldest part as a ridged, curved rod, the juvenile tooth arch, about 1/3 of a volution long, while the rest of the tooth spiral consists of isolated tooth crowns, the roots of which are completely fused. On the ventral side of the compound root is situated abroad, deep groove with a smooth surface. The tooth crowns undergo a gradual change in form from the older to the younger part of the spiral in that their three parts, the proportionally broad cutting blades with serrated cutting margins, the paired middle portions and the paired narrow bases, tend gradually to become more clearly defined. Histologically the tooth-spiral consists of a thin outer layer of enameloid substance covering a layer of pallial dentine, both restricted to the tooth crowns, and an inner core of osteodentine composed of dentitions and an interdentonal bony substance. The anterior part of the head is devoid of scales. (from Bendix-Almgreen 1966)

Type specimens : Idaho no .4 University of Idaho, Moscow Idaho (Bendix-Almgreen 1966)

Type Stratum: Phosphoria Formation (Wordian-Capitanian), south east Idaho, USA

(Bendix Almgreen 1966)

H. cf. *ferrieri*

Description

Helicoprion cf. *ferrieri* is represented by a single specimen. This specimen is 3 1/6 of a tooth spiral. The specimen is very similar to *H. ferrieri* except for the narrowed bases of the tooth crowns. In younger teeth of *H. ferrieri* the narrowed bases are long, slender with nearly parallel upper and lower borders that have a rounded tip and reach a point below the front margin of the idle part of the second tooth crown in front while in *H.* cf. *ferrieri* they are short, almost triangular in shape, with a pointed tip and only reach to just behind the front of the first adjacent tooth. (from Bendix-Almgreen, 1966)

Specimen number: Idaho no. 8 University of Idaho, Moscow, Idaho. (Bendix-Almgreen 1966)

Stratum: Phosphoria Formation (Wordian-Capitanian), south east Idaho, USA (Bendix-Almgreen 1966)

H. ergassaminon Bendix-Almgreen, 1966

Diagnosis

The endoskeleton consists of cartilage with a superficially situated layer of prismatic calcifications. The lower jaw has a high and long, but narrow symphyseal region. A spiral-coiled, strongly calcified symphyseal crest connects with the two halves of the Meckels cartilage, which terminates rostrally along the border of the symphyseal crest. These three elements enclose the symphyseal cavity. The known parts of the dentition are represented by the high, narrow symphyseal tooth spiral, composed of a large number of separated tooth crowns placed on a solid, spiral coiled, undivided compound root, which has on the ventral side a narrow, deep, longitudinal groove with a rough surface. The closely set tooth crowns are long and narrow, and are proximally separated from each other by shallow grooves. Their cutting blades have serrated cutting edges and are a little higher than the middle portions. The middle portions have concave margins. The form of the narrowed based varies from short and stout with angular or evenly rounded terminations, to long and narrow with extremely pointed terminations. Histologically the tooth spiral is composed of osteodentine covered by a thin layer of enameloid substance below which, it is presumed, a layer of pallial dentine was originally present. Parts 3 3/4 volutions of the tooth are preserved. The greatest width of the tooth spiral measures 218 mm.

Type specimen : Idaho no. 5, University of Idaho, Moscow, Idaho. (Bendix-Almgreen 1966)

Type Stratum: Phosphoria Formation (Wordian-Capitanian), south east Idaho, USA

(Bendix Almgreen 1966)

H. sp.

Description

H. sp. is based on the remains of 12 partial, poorly preserved tooth crowns and a part of the compound root, likely from the second tooth volution. Most of the specimen is preserved as impressions in the matrix. The bases are slightly better preserved, thin and can be seen to terminate in a point below the centre of the second tooth crown in front. (from Bendix Almgreen 1966)

Specimen number: Idaho no. 6 University of Idaho, Moscow, Idaho. (Bendix Almgreen 1966)

Stratum: Phosphoria Formation (Wordian-Capitanian), south east Idaho, USA (Bendix Almgreen 1966)

4.3 Canada

4.3.1 Lower Triassic

Polyacrodus Jaekel, 1889

The only specimen of *Polyacrodus* from Canada comes from the Sulphur Mountain Formation, Vega-Phroso Siltstone Member of the Wapiti Lake area of British

Columbia (as do all the specimens described from Canada). This corresponds to the Olenekian (Orchard and Tozer 1997). The specimen consists of a single tooth with a few scattered and hard to identify remains. The specimen has only been identified as *Polyacrodus* sp.

Description:

The tooth conforms to the general *Polyacrodus* (not *Palaeobates*) morphology. It is 6 mm in length but it is only partially preserved and would probably been closer to 10 mm originally. The crown is 2 mm high (though the apex of the main cusp is missing) and the root is approximately 2 mm deep. It is unclear whether the tooth is in labial or lingual view but the crown projects out at the bottom creating a slight overhang over the root. The main cusp is pyramidal and is either vertical or very slightly posteriorly reclining (the matrix obscures some of the detail making it impossible to be sure). There is only one ridge descending from the main cusp that extends into a clear projection on the (labial/lingual) face of the cusp. Besides this ridge the main cusp is free of ornamentation. Only one side of the crown has been preserved. On this side there are 5 visible lateral cusps each getting progressively smaller in size. There may be more very small secondary cusps at the far end giving a serrated like structure to the extreme ends of the teeth. Each of the secondary cusps also has one ridge descending from it and forming progressively smaller pegs. The crown is otherwise free of ornamentation.

The root as previously stated is 2 mm deep (as deep as the crown). In the centre it appears to have a single long row of regular foramina. By the second lateral cusp these foramina cease to be single, clear and long and degenerate into a series of seemingly randomly placed circular foramina. The lower random foramina appear to be bigger than the upper ones.

Specimen number : UAE 19191

Stratum : Sulphur Mountain Formation, Vega-Phroso Siltstone Member (Olenekian),

Wapiti Lake, Canada (Orchard and Tozer 1997)

Contrariodus

There are several specimens of *Contrariodus* from Canada, including two partial vertebral columns with dorsal fins, a caudal fin and an almost complete skeleton.There is only one described species, *Contrariodus wapitiensis.*

Contrariodus wapitiensis De Blanger

Diagnosis:

Species of *Contrariodus* with expanded projection or rear of dorsal fin webbing; relatively slender Meckel's cartilage; possesses epichordal caudal fin supports; Teeth with low wide crown; no labial or lingual peg; no secondary cusps; ventrally extending, non-bifurcating crenelations originating from the longitudinal crest.

Type specimen : UAE 46531

Type Stratum : Sulphur Mountain Formation, Vega-Phroso Siltstone Member (Olenekian), Wapiti Lake, Canada (Orchard and Tozer 1997)

Wapitiodus

There are also several specimens of *Wapitiodus* from Canada, including a partial vertebral column with dorsal fin, and two almost complete skeletons. There is only one described species which has been named *Wapitiodus wapitiensis.*

Wapitiodus wapitiensis De Blanger

Diagnosis:

Body short and robust, dorsal finspines comparatively gracile; anterior teeth with high acuminate cusps and concave crown base; main cusp centrally located with no lateral cusp; ornamentation consists of dense and fine ridges originating from crown-root junction and ascending the crown but not reaching the longitudinal crest; posterior teeth lower and wider than anteriors; main cusp very reduced or absent with no lateral cusp; ornamentation consists of sparse and coarse ridges originating from cusps and terminating at crown/root junction, ridges bifurcating; root of equal or greater depth than crown labial peg poorly defined or absent; lingual peg absent.

Type specimen : TMP.97.74.10

Type Stratum : Sulphur Mountain Formation, Vega-Phroso Siltstone Member (Olenekian), Wapiti Lake, Canada (Orchard and Tozer 1997)

Edestidae

Though there are several well preserved specimens, the edestids from Canada remain undescribed. They bear a superficial resemblance to *Fadenia crenulata* from the Upper Permian of Greenland and it is possible they played the same ecological role in the Lower Triassic Canadian fish assemblage.

4.4 Brazil

4.4.1 Upper Permian

Hybodontiformes indet. Richter and Langer, 1997

The material from the Upper Permian of southern Brazil comes from the Rio do Rasto Formation and consists of one poorly preserved dorsal fin spine (Richter and Langer 1997). There are no preserved teeth and preservation is insufficient to determine which genus of hybodont is present.

4.5 Greenland

4.5.1 Upper Permian

Arctacanthus Nielsen, 1932

There has been some discussion over the possible affinities of *Arctacanthus*. Branson (1933) believed they were rostral teeth while Nielsen (1932) stated that they were spines from chimeroids. Both Woodward (1934) and Bendix-Almgreen (1975) believed that they were cephalic spines from a hybodont. Maisey (1982) stated that while they were considerably more ornate they resembled the "*Sphenonchus*" cephalic spines that have since been identified as probably belonging to *Hybodus* (Cappetta 1987). Specimens assigned to *Arctacanthus* have since been found from the Anisian of Japan where they have also been described as cephalic spines. The base of *Arctacanthus* spines has not been described in the Greenland specimens, though it has in the Japanese specimens where it shows some variation to the standard cephalic spine base type (Gilles Cuny pers. comm. 2005) though not enough to alter the author's opinion on their function. While it is not completely certain that they are cephalic spines, this seems the most likely possibility.

Arctacanthus uncinatus, Nielsen 1932

Description

Material consists of possible cephalic spines. The basal portion of the bilaterally symmetrical spine is expanded and probably at least somewhat deeply inserted. The spine tapering distally; its proximal exerted part is a transverse section resembling a rectangle

the anterior and posterior sides of which are convex, the left and right sides concave; the transverse section of the distal end of the spine sub-oval or elliptic with its longest axis from left to right. On the proximal part of the anterior surface of the exerted part of the spine there is a group of small pointed tubercules; from this group a series of similar tubercules continues distally on each lateral side of the spine towards the extremity of that. (from Nielsen 1932)

Type specimen: No type specimen has been allocated. Specimens have Copenhagen Geological Museum field numbers 127 and 128

Type Stratum: Sect F 120 m above the sea (Wuchiapingian) Kap Stosch, Greenland (Nielsen 1932).

Edestidae

All of the Upper Permian edestid specimens come from the Permian marine fish zone in the upper part of the Posidonia shale member. There has been some discussion over the exact dating of this area with the latest estimate (Stemmerik *et al.* 2001) being Wuchiapingian. In addition to the elasmobranchs, the *Posidonia* shale also contains several genera of actinopterygians (Nielsen 1976) and a diverse brachiopod (Dunbar 1955) and bivalve (Newell 1955) fauna.

Sarcoprion Nielsen, 1952

There has only been one species of *Sarcoprion* identified from Greenland, *Sarcoprion edax*. The material for the species consists of four specimens. The first specimen consists of a large section of the anterior part of the head with a partial dentition. The second is a partial symphyseal whorl withfive teeth, a partial cranial endoskeleton and a number of scales. The last two specimens are an apical section of the cutting blade of the symphyseal whorl and some additional cranial elements and scales. The original description of *Sarcoprion* describes both an upper and lower symphyseal tooth series. All other edestids that have thus far been described possess only a single (lower) symphyseal tooth series that, when the mouth is closed, is housed in a cavity in the upper jaw (Janvier 1996). Given the presence of only one symphyseal series in all other edestids, the presence of a second symphyseal tooth series in *Sarcoprion* seems unlikely though without looking and the original material (that has thus far been unavailable) it cannot be ruled out and as such the entire original description in included below.

Sarcoprion edax Nielsen, 1952

Diagnosis

Head with long and tapering preorbital portion represented by a double-walled capsule of calcified cartilage comprising a neurocranial and a palatoquadratal component fused in a holostylic way. External nasal openings presumably placed about midway

between the double-walled head capsule and a conspicuous longitudinal groove. Lower jaw also consisting of calcified cartilage and an extremely long symphyseal part.

Skin of preserved part of head armed with densely set smaller and larger scales of more or less complicated structure. Dentition comprising a single upper and single lower series of large, mutually fused, symphyseal teeth, numerous lateral series of small simple teeth, and along the lower series of symphsial teeth a pavement of small parasymphyseal teeth. Lower symphyseal series rather strongly curved, though not forming a spiral. Upper symphyseal series almost straight. Crowns of both upper and lower symphyseal teeth with a very strong cutting blade and a long antero-ventro-lateral directed paired lateral division. Roots of symphyseal teeth mainly situated between right and left lateral parts of crown. On basal base of fused roots of lower symphyseal series a broad and deep longitudinal groove. Cutting edges of blades extremely finely serrated. Ornamentation of coronal faces of the crowns of the symphyseal teeth consisted of fine ridges, which on the cutting blades are almost vertical from apex to base, and on the paired lateral parts of the crown form a more intricate pattern. Lateral teeth of the *Orodus-Campodus-Agassizodus* type. All teeth with strongly folded labial and more finely crenulated lingual margin. (from Nielsen 1952)

Type specimen: No type specimen has been allocated. Most complete specimen has Copenhagen Geological Museum field number 214

Type Stratum : Permian Fish zone, *Posidonomya* beds (Wuchiapingian), Kap Stosch. Greenland. (Stemmerik *et al.* 2001)

Erikodus Nielsen, 1952

Erikodus groenlandicus, previously known as *Agassizodus groenlandicus*, is the only species in the genus, which is exclusively found in Greenland. There are several specimens mainly composed of symphyseal teeth but some also containing pieces of calcified cartilage and scales. The main body of the knowledge comes from the largest specimen, which is a series of four symphyseal teeth. Like *Sarcoprion, Erikodus* was also originally described (Neilsen 1952, copied below) as having both an upper and lower symphyseal series. Again some of the original material has thus far been unavailable and as such this cannot be disproved and the entire diagnosis is shown below.

Erikodus groenlandicus Nielsen, 1952

Diagnosis

Dentition comprising an upper and lower series of very large symphyseal teeth and numerous upper and lower series of smaller lateral teeth. Both upper and lower symphyseal series curved, the lower series more strongly than the upper one. Teeth in both series very large and densely set, but not fused mutually as in *Sarcoprion*, *Helicoprion* etc. The individual symphyseal teeth slightly compressed from side to side, with their crown root junction slightly convex and their basal face correspondingly concave from side to side. Crown of symphyseal teeth much lower than the root. Middle portion of crown developed as a blunt elevation, but not as a real cutting blade. Surface of crown ornamented with ramifying sharp ridges. Both labial and lingual margin of the

crown ridged, the labial margin much more strongly so than the lingual one. Lateral teeth of jaws of the same general type as those of *Campodus* and *Agassizodus* and with same serial arrangement. Teeth in foremost and hindmost lateral rows very small, in some of the middle rows especially large. Ornamentation of crowns and folding of coronal margins corresponding closely to those of symphyseal teeth. (from Nielsen 1952)

Type specimen : No type specimen has been allocated. Specimens have Copenhagen Geological Museum field numbers 218-222.

Type Stratum : Permian Fish zone, *Posidonomya* beds (Wuchiapingian), Kap Stosch. Greenland. (Stemmerik *et al.* 2001)

Fadenia Nielsen, 1932

In addition to the *Posidonia* Shale Member, *Fadenia* is also found in the lowermost 2 m of the Schubert Dal Formation that is dated as Changxingian. This is the uppermost Permian elasmobranch find from Greenland. The Schubert Dal Formation is characterised by cool-water carbonates suggesting a drop in temperature towards the top of the Permian (Stemmerik *et al.* 2001). *Fadenia crenulata* is, like *Erikodus groenlandicus,* the only species within its genus and is found exclusively in the Upper Permian of Greenland. There are numerous specimens of *Fadenia* from the Posidonia Shale, most of which consist of symphyseal whorls in various states of completeness but also composed of scales, lateral teeth and a compressed skull.

Fadenia crenulata Nielsen, 1932

Description;

Symphyseal teeth disposed in an unpaired row, not fused with each other, and of bilaterally symmetrical shape. Crown of the symphyseal teeth as normally in the edestids developed in such a way that its right and left halves meet in an acute angle forming a pronounced rostro-caudal edge: the occlusal crest. Crown of the symphyseal teeth at the median plane broader than one half of the length, with the labial margin much and the lingual margin only slightly folded, and with a sculpture of ridges, which, possibly, on account of wear, are much less distinct on the highest median than on the lower lateral parts. Lateral teeth in each half of the jaws arranged in numerous transverse rows; their labial and lingual margins folded, the labial margin however much more intensely folded than the lingual one. The crown of the lateral teeth is not plane, but rises into a cusp situated asymmetrically on the teeth. The root is less strong than that of Agassizodus (now *Erikodus*). (from Nielsen 1932)

Type specimen: No type specimen has been allocated. Specimens have Copenhagen Geological Museum field numbers 129-178.

Type Stratum: Sect F 120 m above the sea (Wuchiapingian) Kap Stosch, Greenland (Nielsen 1932).

4.5.2 Lower Triassic

Polyacrodus Jaekel, 1889

The earlier *Polyacrodus* specimens from Greenland were derived from the Induan fish zone II (Nielsen 1935). This zone is associated with small ophiceratid ammonoids. Though from a different locality, the specimen found in 1992 (described in this work) was probably from the same time period. It was found in the Wordie Creek Formation on the east side of Schuchert Dal, southern Jameson land. This is called "section X" in Perch-Nielsen *et al.* 1972. The concretion was loose in scree but could only have come from one of the 3 concretion horizons near the top of the section. Only one of these yielded fish remains from *in situ* concretions making it the most likely layer to have contained the specimen. The specimen comes from the *Hindeodus parvus* conodont zone. This is the basal conodont zone of the Triassic (Yin 1994). This specimen was also associated with small ophiceratid ammonoids.

There are, thus far, two identified species of *Polyacrodus* from Greenland, *P. twitchetti* and *P.* sp. *P. twitchetti* consists of a partial body fossil preserved to, but excluding, the pelvic fin. *P.* sp. is based on a skull without any associated teeth. There is only one confirmed find of a *Polyacrodus* body fossil (Chapter 2.2) and so information on the skeletal morphology of the genus is limited.

P. twitchetti De Blanger

Diagnosis

Small hybodont shark with a very thin and elongate scapulacoracoid; large mesopterygium; anterior teeth are small ± 1mm; crown low and pyramidal; main cusp centrally placed mesio-distally and higher than lateral cusp; 1-2 pairs of lateral cusp; three ridges descending from main cusp labially; single ridge descending from lateral cusps labially; lingual face largely unornamented but possessing a lingual peg; root subequal to height of crown. Posterior teeth have a poorly developed main cusp with up to 2 pairs of lateral cusp; each cusp has a single ridge descending from it. (De Blanger).

Type specimen : The type specimen is in the Copenhagen Geological Museum but is thus far unnumbered.

Type Stratum : Triassic Fish zone II (Induan), Kap Stosch, Greenland (Nielsen 1952, Yin 1994)

Lissodus Brough, 1935

The only *Lissodus* species (*L. angulatus*) thus far found from Greenland was previously identified as *Polyacrodus claveringensis*. This specimen comes from the same stratigraphic level as the previously mentioned *Polyacrodus* specimens. The only material found was a skull with a partially preserved dentition.

Lissodus angulatus Stensiö, 1921

Diagnosis

Teeth measuring up to 7 mm in length, with moderate central main cusp; lateral cusp absent, but may show incipient development; labial peg moderate. Crown has single ridge descending on main cusp, bifurcating basally into longitudinal ridge along labial crown shoulder. Where known, root is subequal in length to crown and there is an obvious overhang between them. Specialised foramina present along the upper labial root face. All other foramina irregular, but may be organised into longitudinal rows on both lower labial and lower lingual root faces. All teeth long and symmetrical. Lateral teeth relatively narrow with prominent labial peg. Jaw deep and robust with pronounced posterior process. (revised from Duffin 1985):

Type specimen : Reported by Stensiö to be in the collection of Salomon at Heidelberg. Specimen is untraced.

Type Stratum : Fish Horizon 1 (*Posidonomya* bed), *Otoceras/Ophiceras* zone (Induan), Spitzbergen (Duffin 2001)

Aconcinnodus (De Blanger)

Aconcinnodus is a new genus erected to accommodate various species previously assigned to *Polyacrodus* (Chapter 3.1) including specimens previously assigned to *P. claveringensis* (Stensio 1932).

Aconcinnodus claveringensis (Stensiö, 1932)

Diagnosis :

Teeth of the anterior transverse rows with a large main cusp and with one or a few smaller cusps on each side of it. More posteriorly situated teeth with a low pyramidal cusp often or generally asymmetrically located on the crown. An occlusal and a transverse crest always present; a transverse crest also developed on the main cusp of the teeth at least in the posterior or transverse rows. Ornamentation of elevated ridges arranged transversely to the long axis of the teeth; on one side of the crown several long ridges reach from the occlusal crest down to the neck and short ridges also issue both from the occlusal crest downwards and from the neck upwards; on the other side of the tooth, the few or no ridges reach from the occlusal down to the neck, but as a rule only short ridges issue from both the occlusal crest and the neck. Roots of the teeth of the posterior transverse rows bear on one side a strong ridge close below the neck and parallel to the basal margin of the crown.

Type specimen : Stensiö (1932) gives no specimen number though the specimen is believed to be in the collections at Uppsala University.

Type Stratum : Triassic Fish zone II (Induan), Kap Stosch, Greenland (Nielsen 1952, Yin 1994)

Hybodontiformes indet

Hybodontiformes indet. (undescribed)

Description :

Partial and poorly reserved skull, originally attributed to *Polyacrodus* (though not described). No teeth are present in the specimen to confirm this and preservation is insufficient to draw comparisons to *P. twitchetti.*

Specimen number : The specimen is in the Copenhagen Geological Museum but is thus far unnumbered.

Stratum : Triassic Fish zone II (Induan), Kap Stosch, Greenland (Nielsen 1952, Yin 1994)

Parahelicampodus Nielsen, 1952

Like the two genera described above, *Parahelicampodus spaercki* comes from fish zone II in the Kap Stosch region of East Greenland. The material consists of a partially preserved symphyseal tooth whorl.

Parahelicampodus spaercki Nielsen, 1952

Diagnosis

Symphyseal teeth completely fused to a solid, slightly curved rod, the segmented nature of which is indicated by the enamelled tooth-crowns separated from each other by very shallow fissures. Cutting blades of crown large, lateral paired parts of crown narrow and tapering to a point beneath the cutting blade of tooth no. 2 in a forward direction. Labial margin of paired lateral part of crown very slightly ridged, lingual margin smooth. The fused roots protruding very far beyond the basal margin of the coronal series as a shaft, the height of which far exceeds that of *Helicampodus* (Branson). Basal surface of shaft with a broad and narrow longitudinal groove, lateral surface of shaft with an ornament of densely placed, branching , irregular sinuous ridges. (from Nielsen 1952)

Type specimen : Copenhagen Geological Museum Nielsen field no. 102

Type Stratum : Triassic Fish zone II (Induan), Kap Stosch, Greenland (Nielsen 1952, Yin 1994)

4.6 Spitzbergen

4.6.1 Lower Triassic

Hybodus

Three species of *Hybodus* have been found from the Lower Triassic of Spitzbergen (*H. microdus, H. sasseniensis* and *H. rapax*). All are based on isolated teeth

and where originally described by Stensiö 1921.

Hybodus microdus Stensiö, 1921

Diagnosis (from Birkenmajer and Jerzmanska 1979)

Isolated small teeth 0.6 to 2.5 mm, sometimes up to 3.5 mm long. Heterodonty strongly marked. Symphyseal and parasymphyseal teeth with large central cusp and small lateral cusps. Narrow longitudinal depression covered with smooth enamel occurs at the labial side of the crown base. Gradual height reduction of the central cusp is observed in successive tooth rows: the lateral teeth have low, long crown with characteristic large lingual process, sometimes less pronounced as a buttress. Root strongly adjoining to the crown in every tooth.

Type specimen : PMU P.53

Type Stratum : Bone bed 33 m above fish horizon (Olenekian), Mt Viking, Spitzbergen

Hybodus sasseniensis Stensiö, 1921

Description (from Birkenmajer and Jerzmanska, 1979)

Teeth from 1 to 7 mm in labio-lingual length with 1-4 lateral cusps. Root and crown bases are flat. Terminal parts of root and crown are curved lingually. Main cusp is either straight or slightly bent lingually and is either oval or circular in cross section. Main cusp can be broad in posterior teeth or more acute in anterior teeth. Ornamentation

of vertical ridges almost reaching tip of cusps. Ridges usually regular but larger teeth have finer ridges at the base of the tooth that are more dense on the labial than the lingual side, Occlusal crest present but disappears on the tip of the main and occasionally lateral cusps. Root is low with several irregular foramina. Torus strong. Root base damaged due to reworking in sediment.

Type specimen : PMU P.39a

Type Stratum : Bone bed 33 m above fish horizon (Olenekian), Mt Viking, Spitzbergen

Hybodus rapax Stensiö, 1921

Description (from Stensiö 1921)

Species based on 2 isolated teeth. 40 mm in mesio-distal length and 40 mm in height. Crown of teeth is bent basally with a concave lower margin. No lateral cusps are present. Main cusp is high and centrally located on the crown but inclined distally. Main cusp is ellipsoidal in cross section. Occlusal crest present but becomes more delicate and disappears distally. Ornamentation of vertical ridges issuing from the basal margin. Ridges are coarser in the centre of the tooth, thinning out towards the mesio-distal extremities and have a thickened proximal ends. Ridges extend to roughly half way up the tooth centrally while reaching to the occlusal crest at the mesial and distal ends. Root is high and thick and wider than the crown. Concave curvature matches that of crown.

Root displays several foramina.

Type specimen : PMU P.41a

Type Stratum : Bone bed 33 m above fish horizon (Olenekian), Mt Viking, Spitzbergen

Acrodus

Three species of *Acrodus* have been found in the Lower Triassic of Spitzbergen (*A. scaber, A. spitzbergensis and A. vermiformis*). All are based on isolated teeth. *A. scaber* and *A. vermiformis* where originally described by Stensiö (1921) while *A. spitzbergensis* was originally described by Hulke (1873) .

Acrodus scaber Stensiö, 1921

Diagnosis (from Stensiö 1921)

Species based on a number of fragmentary isolated teeth. Teeth measure 2-3.5 mm in mesio-distal length and are generally about 1 mm in height. Highest part of crown is located centrally and is angular rather than rounded. Occlusal crest is present. Ornamentation consisting of medium to coarse ridges (depending on tooth position) originating from the basal margin and extending towards the occlusal crest tending towards the central and highest part of the crown. Most centrally located ridges join at a point just below the peak of the cusp.

Type specimen : PMU P.115

Type Stratum : Triassic bone bed (Olenekian), Mount Congress, Spitzbergen

Acrodus spitzbergensis Hulke,1873

Description (from Stensiö 1921)

Teeth between 2 and 12 mm in mesio-distal length. Crowns flat or with slightly raised cusp. Ornamentation consists of a series of transverse ridges starting from and in most cases running parallel to, the occlusal crest. Root is low and, with the exception of smaller teeth, very narrow. The torus is only slightly broader than the crown. Root crown junction is usually straight but can be slightly concave basally.

Type specimen : PMU P.41a

Type Stratum : Bone bed 33 m above fish horizon (Olenekian), Mt Viking, Spitzbergen

Acrodus vermiformis Stensiö, 1921

Description (from Stensiö 1921)

Species based on fragmentary isolated teeth. Largest fragment measures 24 mm mesio-distally and is roughly 5mm in height. Height of crown near uniform along the mesio-distal length with only a slight elevation towards the centre. Occlusal crest present but with an irregular sinuous course. Secondary longitudinal crest is also present caused by joining of ornamentation ridges. Other ornamentation consists of ridges similar to

those seen in *A. spitzbergensis*. Two type of ridges are visible, short and long. The long ridges originate from the basal margin towards the occlusal crest but only join it at the extreme ends of the crown. The long ridges in the middle join together to form the previously mentioned secondary longitudinal crest. The short ridges originated from the occlusal and longitudinal crests as well as the long ridges are almost always at right angles to them. Root is relatively low.

Type specimen : PMU P.98n

Type Stratum : Bone bed 33 m above fish horizon (Olenekian), Mt Viking, Spitzbergen

Lissodus Brough, 1935

The specimens of *Lissodus* from Spitzbergen are limited to five crowns that come from the Olenekian of Mt. Congress. Only one species of *Lissodus* (*L. angulatus*) is present in the Lower Triassic of Spitzbergen.

L. angulatus(Stensiö, 1921)

Diagnosis See chapter 2

Type specimen : Isolated crown, untraced

Type Stratum : Fish Horizon 1 (*Posidonomya* bed) *Otoceras/Ophiceras* zone (Induan)

Spitzbergen (Duffin 2001)

Palaeobates Meyer, 1847

There are two specimens of *Palaeobates* from Spitzbergen (Stensiö 1921) and both are from the Lower Triassic Fish horizon (Olenekian) of Mt. Anderson. The only Lower Triassic *Palaeobates* species is *P. polaris*. The material consists of two specimens both consisting of teeth and dermal denticles, with one containing very poorly preserved sections of the visceral skeleton.

P. polaris Stensiö, 1921

Description:

The original description of *P. polaris* (Stensiö 1921) has no diagnosis. Stensiö described the specimen as having a very deep and robust mandible with a strongly convex lower margin. The upper margin has a obtuse angled process in front of the articulatory fossa. There were likely six transverse rows of teeth. The teeth were low crowned and durophagous. Ornamentation consisted of a visible longitudinal ridge from which dense, fine and branching ridges issued to the basal margin. Stensiö described *P. polaris* as differing from other *Palaeobates* species in that the ridges, issuing from the longitudinal crest in *P. polaris*, anastomose to give a reticulated appearance.

Type specimen : PMU P 107 (Stensiö 1921)

Type Stratum : Lower Triassic Fish zone (Olenekian), Mt Anderson Spitzbergen

Edestid

Description (Birkenmajer and Jerzmanska, 1979)

This edestid record is based on two fragmentary teeth measuring 2 and 3 mm respectively. The teeth have a large labial process. One tooth has two occlusal crests between which there is a furrow. The other has only one occlusal crest. Teeth superficially resemble *Acrodus*. There is a longitudinal depression at the crown root junction. Ornamentation on the lingual side consists of numerous slightly oblique ridges. Larger ridges, some of which bifurcated run from the occlusal crest to the base of the crown. Short faint enamel swellings separate the ridges close to the occlusal crest. The labial side shows deep, occasionally bifurcating, transverse incisions separating strong processes of the crown. The bases of these processes are bent towards the root and fuse with its single, or twin offshoots.

Type specimen : Specimen housed at the Palaeozoology Department of Worclaw university and is referred to only as Sp/31

Type Stratum : Bone bed 33 m above fish horizon (Olenekian), Mt Viking, Spitzbergen

4.7 Germany

4.7.1 Upper Permian

Wodnika Munster, 1843

There has only been one species of *Wodnika* described from the Upper Permian Kupferschiefer (Schaumberg 1982, Holzaphel *et al.* 1984), which corresponds to the Ufimanian. This species is *W. striulata. W. striulata* is based on isolated teeth as well as an almost complete body fossil.

W. striulata Munster, 1843

Description

Wodnika striulata possesses a relatively narrow neurocranium. The quadrate posterior section of the palatoquadrate is low and short so that the jaw joint is not at the posterior of the skull, but rather beneath the postorbital process. Therein *W. striulata* differs before the majority of the Palaeozoic sharks. During its juvenile stage *W. striulata* developed a symphisial tooth series that was later suppressed with progressive growth of the lateral teeth. The interior skeleton of the pectoral fin shows distinct archipterygial features. The bases of the front radials articulate directly with the scapulocorocoid and are not fused to the pro or mesopterygium. The metapterygium is not attached to the scapulocoracoid. The basals are articulated to each other in a straight axis. The rear section is forked and carries short radials on medial side. The pelvic girdle probably consists of two divided elements. The basipterygium is formed from fused basal rods. In

the male, a double axis of little, well calcified, cartilages joins the mixipterygium. Anterior and posterior dorsal fins are triangular. The length of the front spine is not always proportional to the body size of the animal. This probably also applies to the posterior fin. (from Schaumberg 1999)

Type specimen : Located in Munich but no number given

Type Stratum : Kupferschiefer (Roadian), Richelsdorf, Germany

4.7.2 Lower Triassic

Palaeobates Meyer 1847.

There is one species of *Palaeobates* from the Lower Triassic of Germany (Woodward 1889). This is *P. augustissimus* and it was found in the upper Bunter of Rhenish Baveria. This corresponds to the Olenekian.

P. angustissimus Agassiz, 1838

Description

P. angustissimus is based on isolated teeth, fragmentary portions of the jaws sparse disarticulated skeletal elements and dorsal fin spines (Rieppel 1981). Crown measures 9.5 – 12.5 mm in mesio-distal direction and 2.8 – 3.2 mm in labio-lingual direction. The distal teeth have a virtually flat crown with slight elevation towards the

mesial side. There is a longitudinal crest running along the crown surface parallel to the concave labial edge. Fine ridges anatomose to form an almost uniform reticulate ornamentation. The roots have a single row of foramina. Teeth become narrower and more elevated towards the symphysis. The cusp is asymmetrical and more raised towards the mesial side. Ornamentation again consists of fine, anatomosing ridges. The labial edge of the crown is concave with the lingual side being correspondingly convex allowing the teeth to slot together. (from Rieppel 1981)

Specimen number : T 3830 Paläontologische Institut und Museum der Universität Zürich

Stratum : Middle Triassic, Monte San Giorgio, Kt. Tessin, Switzerland (Rieppel 1981)

4.8 Turkey

4.8.1 Lower Triassic

Synechodus Woodward 1888

The only known specimen of *Synechodus* from the Lower Triassic of Turkey is an isolated tooth from the Kocaeli Peninsula described by Thies (1982). This is also the earliest known record of a confirmed neoselachian tooth.

The group collectively known as palaeospinacids or synechodontids comprises forms that range between the Lower Jurassic and the early Tertiary (Maisey *et al.* 2004). The diagnosis of the Synechodontiformes is based largely on a dental character termed the pseudopolyaulacorhize pattern, which consists or a number of vascular openings in

the root. The current specimen (originally described as *Palaeospinax*), from the Lower Triassic of Turkey, has no preserved root making its assignment to the Synechodontiformes uncertain. Furthermore it has been suggested that that *Palaeospinax* should be declared a *nomem dubium* (Duffin and Ward 1993, Thies 1993) and as such the Turkish specimen, as well as all other *Palaeospinax* material should be assigned to *Synechodus*. Maisey *et al.* (2004) challenge this, stating that *S. dubrisiensis* lacks dorsal fin spines while *Palaeospinax* possesses them hence justifying their separation. It is herein considered that P*alaeospinax* is a *nomem dubium* and despite the lack of finspines in *S. dubrisiensis* the Turkish specimen remains assigned to *Synechodous* pending further study.

Synechodus sp.

Description :

Thies (1982) provides no diagnosis for the specimen and describes it as *Palaeospinax* sp. Only the crown was preserved with one high and acuminate main cusp and a single acuminate lateral cusp (though it is likely that there was originally another lateral cusp located symmetrically on the other side of the main cusp). The preserved section is approximately 0.9 mm high. Ornamentation consists of a few very fine rigdes on both the labial and lingual sides. The tooth displays the typical 3 layered enameloid seen in neoselachians.

Specimen no. : Nr.MBG.3889

Stratum : *cristagalli* zone (Olenekian), Triassic outcrop of North village of Tepeköy, Turkey (Thies 1982)

4.9 Armenia

4.9.1 Lower Triassic

Helicampodus Branson, 1934

Only one species of *Helicampodus* has been found from Armenia (Obruchev 1965). This was named *H. egloni.* Zangerl (1981) only describes the locality and time as Lower Triassic of Armenia.

Helicampodus egloni Obruchev, 1965

Description :

The description given by Zangerl (1981) is vague but *H. egloni* appears to be similar to *H. kokeni* (see earlier description) but lacks the wear facets that implied that *H. kokeni* may have had a dual opposing symphyseal dentition.

Type specimen: Unknown

Type Stratum: Lower Triassic, Armenia.

4.10 Angola

4.10.1 Lower Triassic

Lissodus Brough, 1935

There is only one species of *Lissodus* from the Lower Triassic of Angola. This species is *Lissodus cassangensis* Teixeira, 1954 and is based on two partial specimens, one male and one female.

Lissodus cassangensis (Teixeira, 1954)

Diagnosis

Small *Lissodus* attaining sexual maturity at less than 200 mm body length; fin spines with five or six ribs and six or seven posterior retrose denticles; teeth with main cusp approximately twice the height of the rest of crown; occlusal crest indented by one or two ridges weakly defining lateral cusplets: labial peg broad and rounded; cephalic spines with tri-lobed, "convict arrow" shaped basal plate, flattened and rounded marginal lobes, shaft like posterior lobe broadening distally, low main cusp and single pair of low, divergent, triangular lateral cusp; 11 paired ribs; pectoral fin with 1 propterygial radial, three mesopterygial radials and five metapterygial radials; pelvic fin with first three radial articulating with pelvic bar, plus nine basipterygial radials; basipterygial axis consisting of elongate "metapterygium", three radial-bearing basals, plus (in males) four

intermediate segments and mixipterygial cartilages; differs from *L. africanus* in less extreme size of first dorsal fin-spine and in less extensive shagreen. (from Antunes *et al.* 1990)

Type specimen IICT 70 (Instituto de Investigação Científica Tropical)

Type Stratum : Cassange Series (Olenekian), Cama das Peixes, Lutoa Baixa do Cassange, Angola (Antunes *et al.* 1990)

4.11 Madagascar

4.11.1 Lower Triassic

Acrodus Agassiz, 1837

The only *Acrodus* specimen from Madagascar comes from the Amphibole Bay locality, which is dated as Olenekian (Beltan 1996). The material consists of the upper and lower jaws and a partial neurocranium. The specimen was assigned to *Acrodus* based on its teeth but was not described to species level.

Acrodus sp.

Description

Acrodus sp. from Madagascar is based on a cast within a nodule and as such Thomson (1982) was unwilling to erect a new species based on the material. *Acrodus* sp.

has four rows of teeth. Teeth in the first row are markedly smaller than those is subsequent rows which are all of roughly equal size. The teeth of the first and second rows are more strongly curved than those of the last two rows. Ornamentation consists of relatively fine, bifurcating ridges. The palatoquadrate is elongate with a small postorbital expansion and lack any significant thickening at the optic process. The anterior section is a stout bar with a pronounced downward and mesial curvature of the tip and there is a broad ventro-mesial flange bearing the dental battery. The post orbital portion of the lateral surface of the palatoquadrate is concave and massively thickened. The mandible is relatively deep with the main anterior part of the ramus being largely flat. In lateral view the posteroventral part of the mandible appears to be concave but there are no other major features. The branchial skeleton has been badly damaged but some small portions remain. (from Thomson 1982)

Specimen number: MCZ 13432

Stratum : Sakamena Group (Olenekian), Amphibole Bay locality, Madagascar.

Lissodus Brough, 1935

The Lower Triassic record of *Lissodus* in Madagascar is based on several specimens. There are Three specimens of *Lissodus* aff. *cassangensis* from the Olenekian of North western Madagascar. Two of the specimens are anterior body sections in lateral perspective with portions of the neurocranium, jaws, branchial arches, vertebral column,

dorsal and pectoral fins but no pelvic anal or caudal fins. The third is in dorsal view and has a preserved neurocranium, vertebral column and dorsal fin spines.

Lissodus aff. *cassangensis*

Description

Lissodus aff. *cassangensis* is very similar to *Lissodus cassangensis* (Antunes *et al.* 1990) but is described based on imprints rather than preserved skeletal material. For a full description see chapter 2.2.1.

Specimen number: The specimen is in the Copenhagen Geological Museum but is thus far unnumbered.

Stratum : Sakamena Group, Olenekian, Madagascar.

Hybodontiformes indet.

A final specimen from Madagascar is a well preserved pelvic fin. The specimen does not have any associated teeth or enough information to assign it to generic level so remains Hybodontiformes indet.

4.12 South Africa

4.12.1 Lower Triassic

Lissodus Brough, 1935

Originally described by Broom in 1909, there are several specimens, both teeth and articulated skeletons, of *Lissodus* from the Lower Triassic of South Africa. The type locality is Becker's Krall, Rouxville, Orange Free State and the Upper Beaufort Series (Karroo System) corresponds to the Olenekian. There is only one species of *Lissodus* from South Africa, the type species, *L. africanus*.

L. africanus (Broom, 1909)

Diagnosis

Both jaws are fairly deep and relatively solid. The lower jaw is deep posteriorly, tapering rapidly anteriorly, and rounded towards the symphysis. The upper jaw is deep along much of its length. Cephalic spines are present behind the orbit in the male. The notochord persists. The neural arches, transverse processes and haemal arches are calcified. The neural spines are moderately long, tapering to a point dorsally in examples from the anterior region of the vertebral column. The transverse processes are slender in shape. Moderately long and delicate ribs are located behind the pectoral girdle. The pectoral girdle comprises two stout, elongate and narrow scapulo-coracoid bars which are not fused ventrally. Each scapula is attached to the base of the first dorsal fin spine. The

pectoral fins are fairly large. Claspers are present in the male. The dorsal fins are supported by costate, stout fin spines of hybodontiform organisation each possessing a double row of denticles on the posterior margins. The first dorsal fin spine is the shorter and the stouter, lying at 45° to the body in lateral view, with the basal plate not being surmounted by radials. The second dorsal fin spine is straighter (70° to the body in lateral view) with a similar triangular basal plate attached to the spine base, and a row of several delicate radials further supporting the fin. (from Duffin 1985)

Type specimen : SAM 1082

Type Stratum: Karoo (Olenekian section), Becker's Kraal, Rouxville district, Orange Free State, South Africa

4.13 Russia

4.13.1 Upper Permian

Original descriptions for all Upper Permian shark taxa from Russia are unavailable. Three species are listed in Minikh and Minikh (1996) and these will be mentioned below. All of the specimens described below come from continental freshwater beds, this draws into question the validity of some of the generic assignments (*Polyacrodus* has not been found in fresh water anywhere else in the Triassic).

Hybodontiformes *indet* Zangerl 1981

These specimens that were originally assigned to *Polyacrodus* sp. consist of a number of teeth and fin spines found from the East European Platform, Vologda and Moscow districts (Minikh and Minikh 1996). This corresponds to the Wuchiapingian to the Changhsingian. No accurate description is given for the teeth and fin spines are not identifiable to generic level. The specimens are therefore reassigned to Hybodontiformes indet. as there is insufficient evidence to support their assignment to *Polyacrodus*.

Hybodontiformes *indet* . Zangerl 1981

There are a number of teeth from the Upper Permian of Russia that were previously assigned to *Lissodus*. Rees and Underwood (2002),however, cast doubt on the generic assignment claiming that the combination of a mesio-distally expanded crown and a strong crown shoulder separated the genus from *Lissodus*. Rees and Underwood (2002) did not assign the specimens to another genus, merely referring to them as Palaeozoic genus 2. Without sufficient evidence to justify an assignment to *Lissodus* or a suitable alternative genus in which to place this species, they are assigned to Hybodontiformes indet.

Elasmobranchii *incertae sedis*

Like the specimens assigned by Minikh and Minikh (1996) to *Polyacrodus* and *Lissodus* these specimens, originally described as *Wodnika* sp. come from the East European Platform, Vologda and Moscow districts and consist of teeth and fin spines (Minikh and Minikh 1996). No description is given to justify the assignment to *W.* sp. and therefore it cannot be accepted.

Elasmobranchii *incertae sedis*

Ivanov (2000) mentions the remains of several palaeospinacid teeth from the Wordian to the Capitanian of Russia. There are no available illustrations but the teeth are described as having crowns that are strongly inclined lingually with the bases of the cusps fused. The labial face of the cusp is flat and ornamented by irregular ridges. The main cusp has well developed lateral cutting edges and the basal face of the tooth is concave. Ivanov describes the teeth as being similar to those of *Synechodus* with a few differences keeping him from assigning them to the genus. There is however no description of the root in any of these teeth nor is there any description of the structure of the enameloid. With no illustaration, confirmation of a triple-layered enameloid or the presence of pseudopolyaulacorhize pattern these teeth cannot be accepted as palaeospinacid.

Xenacanthidae *indet.*

Both Ivanov (2000) and Tverdokhlebov *et al.* (2005) mention the presence of xenacanth shark remains assigned to *Xenosynechodus egloni* in the Lopingian of Russia. The material consists of fragments of jaw as well as teeth and spines, however neither works offers either a description or an illustration of the material. The original description (Gluckman 1980) in which the family and genus were erected (based on the same material) is unavailable. With such a lack of information the validity of both the family Xenosynechodontidae and the genus *Xenosynechodus* cannot be accepted and the material is herein assigned to Xenacanthidae *indet.*

4.13.2 Lower Triassic

The hybodont material from the Lower Triassic of Russia consists of a number of dorsal fin spines (Minikh 1985). There are six spines in total. These were originally assigned to two different species *H. spasskiensis* and *H. maximi,* each being represented by three spines. No diagnoses were provided by Minikh (1985) so the entire (fairly short) descriptions are below. To date there is no accepted classification scheme that would allow the assignment of hybodont material to genus or species level based on isolated finspines (Cuny pers. comm.. 2004). The validity of the assignment therefore cannot be accepted and *Hybodus spasskiensis* and *Hybodus maximi* are herein assigned to Hybodontiformes indet. A and B respectively.

Hybodontiformes *indet* A Minikh, 1985

Description

Small weakly curved spines, with wedge-shaped parabolic cross section in area of lower caudal denticles. Ribs long, ending far below tip of longitudinal hollow (basal aperture, according to Maisey). Anterior (axial rib) longest, rather high and sharp. Distance between ribs unequal, increasing to almost twice that between three anterior ribs in proximal part. Number of ribs at distal end of spine three or four, increasing to six or seven towards proximal end. Additional ribs appearing in intervals between previous ribs, but not as a result of bifurcation. Caudal surface weekly convex, with two rows of transversely orientated denticles. Wavy, longitudinal groove running between denticles. Longitudinal hollow half as long as spine or somewhat more. Root short, occupying less than one third length of spine. Angle of inclination of fin spines about 40°. (from Minikh 1985)

Specimen no. : SGU 104-B/910

Stratum : Lower Triassic (Olenekian). Kuybyshev, Gor'kovskaya and Orenburg oblasti (Minikh 1985).

Hybodontiformes *indet* B Minikh, 1985

Description

Thin, slender spines, in transverse section, a narrow parabola in each area of lower caudal denticles. Lateral surface of spine with 10-12 ribs on each side; at tip of spine. Original number of ribs almost half as many (4 – 5). Increase in number of ribs by bifurcation. Intervals between ribs equal to width of ribs (or somewhat wider). All ribs long, extending much lower than tip of longitudinal hollow. Longest rib is the anterior one . Caudal surfaces very weekly convex, with two (sometimes one) rows of alternately arranged denticles. Longitudinal hollow occupying more than half, and root from one fourth to one sixth length of spine. Angle of inclination of spine about 30°. (from Minikh 1985)

Specimen no.: SGU 104-B/901

Stratum : Yarenskiy horizon (Olenekian) Arkhangel'sk Oblast and Komi ASSR;

Petropavlovsk Formation (Olenekian) Orenburg Oblast' and Bashkirian ASSR (Minikh 1985)

4.14 Pakistan

4.14.1 Upper Permian

Helicampodus Branson, 1935

The *Helicampodus* specimen comes from the upper *Productus* limestone in the Salt Range, Pakistan (Branson 1935). The specimen has been assigned to *H. kokeni*. The material consists of a single partial symphyseal tooth whorl.

H. kokeni Branson, 1935

Description :

Zangerl (1981) described the symphyseal teeth as being much the same as those of *Sarcoprion* but with the crown spurs and bases pointing backwards. There are wear facets on the holotype that suggest a dual set of opposing teeth though this may be due to an abnormality in the opposing teeth.

Type specimen : Unknown.

Type Stratum : Upper *Productus* Limestone, Upper Permian, Salt Range, Pakistan

4.15 India

4.15.1 Lower Triassic

Triodus Beyrich, 1848

There has, to date, been only one species of *Triodus* found from India and this was based on a single tooth. This was originally described as *Xenacanthus* sp. but Hampe (2003) suggests that Triassic xenacanths are better attributable to *Triodus*. The specimen comes from the *Otoceras* zone of the Shalshal area of Kumaun, Himalaya. This section was described as Lower Triassic by Mehrotra *et al.* (1981), but no stage name was given.

Triodus sp. Mehrotra *et al.*, 1981

Description

The tooth is fairly robust and has both crown and root preserved. It bears a slight resemblance to *T. indicus* (Jain 1980) though its central cusp is shorter and more robust. It has also been compared (Mehorta *et al.* 1981) to *O. compressus* and *O. texensis* but differs from both of these in having diverging lateral cusps. (from Mehorta *et al* 1981)

Specimen number : No number given

Stratum : Lower Triassic *Otoceras* zone, Shalshal area, Kumaun, Himalaya, India

(Mehorta *et al.* 1981)

Acrodus Agassiz, 1837

Only one species of *Acrodus* has been found in India though it has been found in several locations including the *Otoceras* zone of the Shalshal area of Kumaun, Himalaya (Mehrotra *et. al* 1981) and the Early to Late Triassic from the Guryul Ravine and Khreuh sections of Kashmir, Himalaya (Sahni and Chabra 1976). The species was described as *A. substriatus* which, despite the ambiguity in the description below (it states that the teeth have a smooth crown with bifurcating ridges), is here considered to be valid. Only isolated teeth have been found. As above, the sections which yielded the fossils are simply described as Lower Triassic without an accurate stage name.

A. substriatus Schmid, 1861

Description

The teeth are characterised by an elongated and smooth crown. The crown is slightly elevated in its central region. In the middle of the crown, there is a ridge running all along the lower axis of the crown. From the ridge, begin innumerable bifurcations of vertical ridges. The base possesses a number of parallel ridges. (from Mehorta *et al.* 1981)

Specimen no.: No specimen number given.

Stratum: Khreuh and Guryul Ravine sections (Lower Induan), India

4.16 China

4.16.1 Upper Permian

Helicoprion Karpinsky 1889

The only specimen of *Helicoprion* from the Upper Permian of China comes from the Dalong Formation, Maanshan district of Jiahe, Hunnan. The specimen consists of a partial tooth whorl and was described as *Sinohelicoprion macrodontus* Lei, 1983. While Lei provides a brief diagnosis of the species (below) he does not provide any description of the genus *Sinohelicoprion* nor does he state what separates it from *Helicoprion*. The characters listed within Lei's diagnosis such as serrated cutting blade, wide and short lateral wing (lateral tapering parts in Bendix Almgreen 1966) that narrows forward and the histological description are all consistent with specimens of *Helicoprion* (Bendix Almgreen 1966). The diagnosis below does not list any features that would justify a separation of the two genera and the specimen is therefore herein considered to be *Helicoprion macrodontus*.

Helicoprion macrodontus Lei, 1983

Diagnosis

Teeth of cutting type, laterally compressed; cutting blade serrated anteriorly and posteriorly, abrasion surface lacking; lateral wing relatively wide and short, without

differentiation into lower and middle parts, no serration on the anterior and posterior margin, the base of lateral wing narrowing forward; tubular osteodentine layer thin, fibrous osteodentine layer spreading into cutting blade, spongy osteodentine layer absent; canal on tooth row base shallow and broad; size teeth very large.

Type specimen : YIGH-V25146

Type Stratum : Dalong Formation (Upper Permian), Maanshan district of Jiahe, Hunnan China.

4.16.2 Lower Triassic

Ctenacanthidae ***indet.*** Agassiz, 1837

Several isolated teeth have been found from the Lower Triassic Loulou formation. Some of these teeth have been assigned to *Hybodus yohi* and *Hybodus zuodengensis,* this assignment is however highly suspect. Both the description and the illustration depict teeth that have several cladodont type features such as the multicuspid crown with a prominent central cusp and a thin, near horizontally, inclined root. Cladodont teeth have been found in a number of taxa (including the Cladoselachidae, Ctenacanthidae and the Symmorididae) from the Devonian to the Upper Permian but this is the first record from the Lower Triassic. It is possible that the teeth represent the first known Lower Triassic ctenacanth and, though without additional material, it is impossible to be sure, the teeth

described as *Hybodus yohi* and *Hybodus zuodengensis* are therefore considered as Ctenacanthidae indet A and B respectively.

Ctenacanthidae indet. A Yang *et al.*, 1984

Description

Dentition heterodont, main cusp high, slender and arched lingually; maximum three pairs of lateral cusps; cross section of central and lateral cusps elliptical; labial face of crown with undeveloped ridges but lingual face of crown with weakly developed ridges covering two-thirds of central cusp; root low with weakly bent centre; labial face of root without any nutrient foramina but lingual and basal face of the root with numerous small and rounded or creviced nutrient foramina.

Specimen no. : PU 83018 (Peking University)

Stratum : Luolou Formation (Olenekian). Zuodeng district, Tiandong County of Guangxi Zhuang Autonomous Region, China.

Ctenacanthidae indet. B Yang *et al.*, 1984

Description

Dentition heterodont; main cusp slightly high, four cusps on one side of main cusp and three on the other; cross section of main and lateral cusps roughly triangular; tooth crown with developed ridges particularly on the labial face of the crown; a groove

between labial face of tooth crown and root; root low; labial and lingual faces with small rounded nutrient foramina.

Specimen no. : PU83008 (Peking University)

Stratum : Luolou Formation (Olenekian). Zuodeng district, Tiandong County of Guangxi Zhuang Autonomous Region, China.

Lissodus Brough 1935

There has been one specimen assigned to *Polyacrodus* from the Lower Triassic of China but this assignment is also questionable. The illustration and description suggest a morphology more consistent with *Lissodus* i.e. a pronounced labial peg. It it therefore herein reassigned to *Lissodus tiangdongensis*

Lissodus tiandongensis Wang *et al.*, 2001

Emended diagnosis

Tooth massive and expanded transversely; main cusp more or less pyramidal, low, blunt and expanded both labially and lingally; the labial face of the main cusp has an expanded peg; both the labial and lingual faces of the main cusp have high crests. Lateral cusps undeveloped, Main cusp possessing an occlusal crest and lateral sides possessing an occlusal crest and transverse occlusal crests though both crests are weak.

Type specimen : IVPP V 12670 (Institute of Vertebrate Paleontology and Paleoanthropology)

Type Stratum : Luolou Formation (Olenekian). Zuodeng district, Tiandong County of Guangxi Zhuang Autonomous Region, China.

4.17 Japan

4.17.1 Upper Permian

Helicoprion Karpinsky, 1899

Only one specimen of *Helicoprion* has been found from the Upper Permian of Japan and described by Araki (1980) but the preservation was inadequate to identify it to species so it was classed as *H.* sp. Illustrations (Goto 1994, Goto *et al.* 1996) show that the specimen consists of an incompletely preserved tooth whorl with the partial remains of three volutions.

Type specimen : specimen no. unknown.

Type Stratum : Konokura Formation (Upper Permian) Kamiyatsuse, Kesennuma City, Miyagi Prefecture, northeast Honshu, Japan

Helicampodus

Teeth of *Helicampodus* sp. were reported from the Toyoma Formation of northeast Honshu by Uyeno et al in an oral presentation given in 1979 and later referred to by in several papers by Goto (1994, Goto *et al.* 1996) though no written description seems to exist.

Specimen number : Specimen number unknown.

Stratum : Toyoma Formation (Upper Permian) Toyomacho, Toyoma-gun, Miyagi Prefecture northeast Honshu, Japan.

Orthacanthus Agassiz, 1843

Orthacanthus sp.

Description

The specimen consists of an incomplete isolated tooth. The preserved part is one of the two lateral cusps. The cusp is slender and curves to the inner or outer side one quarter of the way up its length. Each side of the cusp is serrated. There is a shiny black enameloid layer on the tooth. The total length of the cusp is 12.4 mm and it has a maximum width of 2.1 mm.

Specimen number: GSJ F15014 (Geological Survey of Japan)

Stratum : Senmatsu Formation (Upper Permian), Kanoko, Motoyoshi Town, Miyagi Prefecture, South Kitakami Belt, northeast Japan.

Hexanchidae indet

A single tooth of a hexanchoid specimen (genus and species unknown) was found in the same area as the aforementioned *Helicampodus* specimen by a Mr. K. Harada and reported in an oral presentation by Koizumi (1991). This tooth is referred to in several subsequent works (Goto 1994, Goto *et al.* 1996) but no written description is known.

Specimen number: Specimen number not known

Stratum : Blach shale of the Kashiwadiara Formation, Takakurayama Group (Capitinian) Yotsukura, Iwaki City, Fukushima Prefecture, northeast Japan.

4.17.2 Lower Triassic

Lissodus Brough, 1935

The only Lower Triassic shark specimens thus far recorded from Japan belong to the species *Lissodus minimus* Agassiz ,1834. This species is represented entirely by

isolated teeth. Previously thought to be restricted to the Upper Triassic (Duffin 2001), these teeth where found in Taho, Shirokawacho, Higashiuwa-gun, Ehime Prefecture Shikoku, in the Taho Formation, which Goto *et al.* (1996) identifies as Lower Triassic. There are some minor doubts concerning the assignment of the Japanese specimens to *Lissodus minimus*. The doubts arise because the Japanese teeth are larger than any other *L. minimus* teeth described (Cuny pers. comm. 2004) and because they are found in the Lower Triassic while all other specimens have been found from the Rhaetian. While the size difference and extension of the stratigraphic range is unusual I do not believe this is sufficient to assign the Japanese material to a different species and they therefore are herein considered to remain in *L. minimus*.

Lissodus minimus Agassiz, 1839

Diagnosis

Teeth of *Lissodus* up to 7 mm long, showing moderate heterodonty. The main cusp is highest in mesial and anterolateral teeth. The labial peg is well developed in mesial teeth, but becomes progressively weaker laterally through the dentition. The occlusal crest is moderate. Lateral cusp may be developed. The crown is robust and low in lateral teeth. The crown may be ornamented by moderate vertical ridges. The crown/root junction is deeply incised in mesial teeth, but becomes progressively less so laterally. Specialised foramina present. (from Duffin 1995)

Specimen no.: No specimen numbers are given but the repository is Tsurumi University

Stratum : Taho Formation (Scythian), Japan

5.1 Global diversity change of sharks over the P-TR boundary

5.1.1 Introduction

This section outlines the changes in shark diversity over the P-Tr boundary on a global scale (regional information is available in chapter 4.0). Changes and turnover of families genera and species will be considered. It is important to examine the total effect of the P-Tr mass extinction as well as the local effects in order to gain an idea of the relative impact the event had on sharks in comparison to the other groups. While as complete as is possible several factors could affect the accuracy of this section. The relatively low preservational potential of cartilaginous fish, the tendency to over-split shark taxa, the current ambiguity of several genera and species and the apparent lack of Uppermost Permian and Lowermost Triassic shark yielding fossil localities could all contribute to a decline in the accuracy of the conclusions drawn.

5.1.2 Upper Permian

5.1.2.1 Roadian

Shark diversity in the Roadian is low with only two genera and three species, which come from two localities, one in Western Europe and the other in North America. The first species is *Wodnika striatula* from the Richelsdorfer Kupferschifer, Germany. The other two species and the xenacanths *Orthacanthus texensis and O. platypternus*, and both found in the Wichita Group of Texas.

5.1.2.1 Wordian – Capitanian.

The diversity of named species (five specimens are not assigned species names) decreases in the Wordian to Capitanian as did the number of genera. The specimens from these periods were found in North America and Russia. Those from North America were assigned to the eugeneodont genus *Helicoprion*. The two named species are *H. ferrieri* and *H. ergassimion* with to other specimens being described as (*H.* cf. *ferrieri* and *H.* sp). The specimens found in Russia were originally described as *Xenosynechodus egloni* and *Xenosynechodus* sp. There is insufficient evidence to support this and they are herein considered to be Xenacanthidae *incertae cedis* A and B respectively (See chapter 4).

5.1.2.3 Wuchiapingian – Changhsingian

Specimens from these periods are divided into two groups, those that were found exclusively in the Wuchiapingian and those that are described from areas with less accurate stratigraphy, described as being Wuchiapingian to Changhsingian.

There were five genera found exclusively in the Wuchiapingian, these came from Greenland and Japan. The only specimen from Japan was a partial eugeneodont (*Helicoprion* sp.) tooth whorl from Konokura Formation. Of the Greenland sharks, three were eugeneodonts (*Fadenia crenulata, Erikodus groenlandicus* and *Sarcoprion edax*) and one was a hybodont (*Arctacanthus uncinatus*) all from the Kap Stosch region.

The specimens that are aged Wuchiapingian – Changhsingian come from two genera with none having been described to species level (there are four specimens that are not assigned to genus level). All the sharks from these periods were found in either

Russia or Japan. Of the specimens from Russia one (originally described as *Wodnika* sp.) is herein considered Ealsmobranchii *incertae sedis* and two are hybodonts (originally described as *Lissodus biggibus* and *Polyacrodus* sp.) considered herein as Hybodontiformes indet. A and B respectively (see Chapter 4). All of these specimens come from the East European Ural platform. Of the specimens from Japan one is a xenacanth (*Orthacanthus* sp.) from the Senmatsu Formation and the other is a eugeneodont (*Helicampodus* sp.) from the Toyama Formation.

In addition to these, a specimen assigned to *Helicoprion macrodontus* was found from the Changhsingian from China and finally there is one specimen whose stratigraphic position is described only as Upper Permian. The specimen is a hybodont finspine (Hybodontiformes indet.) from Brazil.

5.1.3 Triassic

5.1.3.1 Induan

There is thus far only one area that has yielded shark material from the lowest Triassic (Induan), Greenland. Specimens studied from this area have been assigned to four genera and species. The first three of these species are hybodonts (*Polyacrodus twitchetti, Acconcinodus claveringenssi* and *Lissodus angulatus*). The final species described from the area is a eugenodont (*Parahelicampodus spareki*).

5.1.3.2 Olenekian

By far the most diverse stage in the period is the Olenekian which has specimens assigned to nine genera and 16 species (with several specimens not being described to species level). The vast majority of these species are hybodonts.

The first species to be mentioned from the Olenekian (*Wapitiodus wapitiensis*) was found from Canada and has yet to be assigned to a family. There are three species of *Hybodus* (Family Hybodontidae). *Hybodus rapax, Hybodus sassiensis* and *Hybodus microdus*, all found in Spitzbergen.

The Olenekian has five sharks from the family Acrodontidae, all from the genus *Acrodus*. Three species (*Acrodus scaber, Acrodus spitzbergensis* and *Acrodus vermiformis*) were found from Spitzbergen, *Acrodus substriatus* was found in India and a specimen described only as *Acrodus* sp. was found from Madagascar.

Another family of hybodonts that is well represented in the Olenekian is the Lonchidiidae. This family is represented by five named species (all from the genus *Lissodus*), from several localities around the world. *Lissodus angulatus* (also previously found from the Induan of Greenland) was found in Spitzbergen. *Lissodus africanus* (the type species of the genus) was found in South Africa, *Lissodus minimus* in Japan and *Lissodus cassangensis* and China yielded specimens of *Lissodus tiandonensis*. Several specimens assigned to *Lissodus* aff. *cassangensis* were discovered in Angola and Madagascar respectively.

The final hybodont family to be discovered from the Olenekian was the Polyacrodontidae. In the Olenekian this family is represented by three genera (*Palaeobates, Polyacrodus* and *Contrariodus*) and three named species from three

different localities. *Palaeobates polaris* was discovered in Spitzbergen while *Palaeobates angustissimus* was found in Germany. The final named polyacrodont species is *Contrariodus wapitiensis* from Canada. A specimen of *Polyacrodus* sp. was also found in Canada

In addition to the hybodonts there were also representatives of other shark groups (previously thought to have gone extinct over the P-Tr) in the Olenekian. Two different areas (Spitzbergen, and Canada) have yielded specimens of eugeneodonts (though both remain thus far undescribed) and a specimen of *Helicampodus* was discovered in the Lower Triassic (though no stage was given) of Armenia. In addition to this, specimens of the xenacanth (*Triodus* sp.) have been found from India and two unidentified ctenacanths (previously described as *Hybodus zuodengensis* and *Hybodus hoyi)* were found from the Olenekian of China.

Finally the earliest well recognised discovery of a neoselachian (*Synechodus* sp.) comes from the Olenekian of Turkey.

5.1.4 Discussion

When examining the diversity trends it should be noted that while the above reflects the diversity of sharks that have thus far been found in the Upper Permian and Lower Triassic, several other genera must have been present. If the taxa found in the Lower Permian are examined it can be seen that several genera are present but then are not seen again in the fossil record until uppermost Permian or Triassic. Genera missing from the fossil record in the Roadian include *Acrodus, Lissodus, Aconcinnodus,*

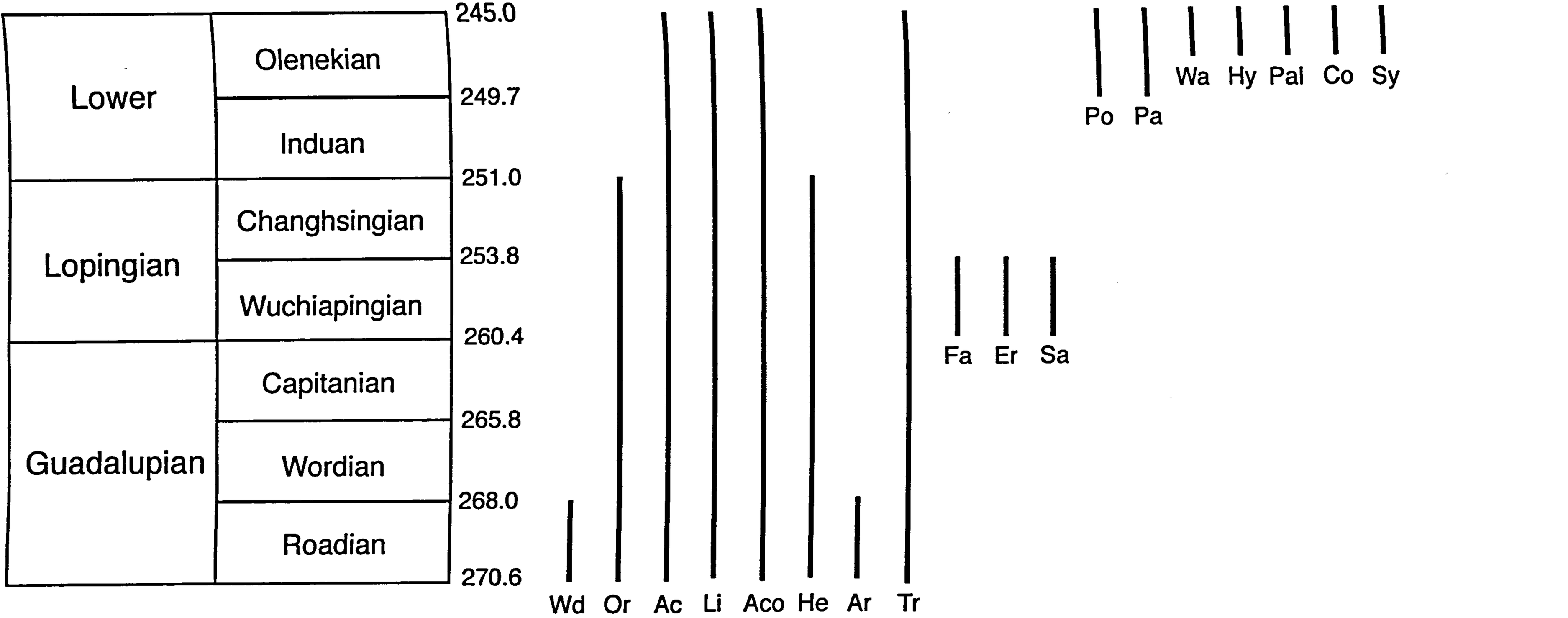


Fig 3.2. Range chart of genera over the Upper Permian and Lower Triassic. Wd = Wodnika, Or = Orthancanthus, ,Ac = Acrodus, Li = Lissodus, Aco = Aconcinnodus, He = Helicoprion, Ar = Arctacanthus, Tr = Triodus, Fa = Fadenia, Er = Erikodus, Sa = Sacroprion, Po = polyacrodus, Pa = Parahelicampodus, Wa = Wapitiodus, Hy = Hybodus, Pal = Palaeobates, Co = Contrariodus, Sy = Synechodus.

Helicoprion, Arctacanthus, and *Triodus*. In addition to the genera found in the Wordian – Capitanian there should be occurrences of *Acrodus, Aconcinnodus, Lissodus, Arctacanthus, Orthacanthus* and *Triodus*. The fossil record of the Wuchiapingian – Changhisgian has four genera missing (*Acrodus, Lissodus, Aconcinnodus* and *Triodus*). The fossil record of the Lower Triassic is relatively more complete with only two genera being missing from the Induan (*Acrodus* and *Triodus*) and one from the Olenekian (*Aconcinnodus*). If it is assumed that there must have been at least one species from each missing genus, this then alters the minimum number of genera and species in each period, as shown in Fig. 3.3.

The data for the minimum amount of genera and species were subjected to statistical analysis using the Chi squared test for significance. The test shows that at the 95% level there is no significant pattern shown by the above data. This test should, however, be viewed carefully considering the low values within the data generated by the biasing factors named at the beginning of this chapter namely the relatively low preservational potential of cartilaginous fish, the current ambiguity of several genera and species and the apparent lack of Uppermost Permian and Lowermost Triassic shark yielding fossil localities. Despite the lack of statistical significance the following broad patterns can be seen.

No named species crosses the P-Tr boundary though this is not unexpected as the tendency for taxonomic splitting when naming shark species means that it is uncommon for sharks to be found in several stages. Despite the lack of species survival at least five

families (Polyacrodontidae, Acrodontidae, Lonchididae, Edestidae and Xenacanthidae) survived, with only two (Agassizodontidae and Caseodontidae) going extinct. It is possible that one of more of the thus far undescribed eugeneodonts from the Olenekian may belong to either the Agassizodontidae or the Caseodontidae thus further increasing the survival rate.

The surviving families consisted of seven genera (*Acrodus, Polyacrodus, Lissodus, Acconcinodus, Triodus* and *Helicampodus*) all of which crossed the P-Tr boundary. As can be seen, the minimum number of genera decreases slightly from the Roadian – Capitanian but then sees a jump from nine to 11 in the Wuchiapingian – Changhisgian before dropping to six (45% reduction) in the Induan. The Olenekian sees a diversification to generic diversity levels comparable to those of the uppermost Permian. The pattern is much the same in species diversity, though the diversity in the Olenekian is far higher (almost double) than pre-extinction levels. The increase in the number of genera and species in the Wuchiapingian – Changhsingian and the subsequent drop over the P-Tr boundary is largely due to eugeneodonts. The presence of four new eugeneodont genera (*Helicampodus, Sarcoprion, Erikodus* and *Fadenia*) in addition to the *Helicoprion* causes a marked increase in Upper Permian shark diversity and the extinction of all but *Helicampodus* over the P-Tr boundary results in a substantial loss of diversity. The most notable change to diversity patterns caused by hybodonts is seen in the Olenekian where there are four new genera and an increase in species numbers to at least 17. The diversity of xenacanths and other shark groups remain relatively constant over the study period and do little to change diversity patterns.

If we were to accept the taxonomic assignments that have been rejected (chapter 4) due to lack of information (i.e. *Xenosynechodus egloni* and *X* sp. from the Wordian – Capitanian of Russia, *Wodnika* sp., Palaeospinacidae indet., *Lissodus biggibus* and *Polyacrodus* sp. from the Upper Permian of Russia and *Hybodus zuodengensis* and *H. yohi* from the Olenekian of China) it would do little to alter the discussed pattern. *Xenosynechodus*, having been re-assigned to Xenacanthidae indet. is assumed to contain at least one genus and species of xenacanth and hence would not add to the diversity estimate. *Polyacrodus* and *Lissodus* are assumed, due to ghost ranges, to be present in the

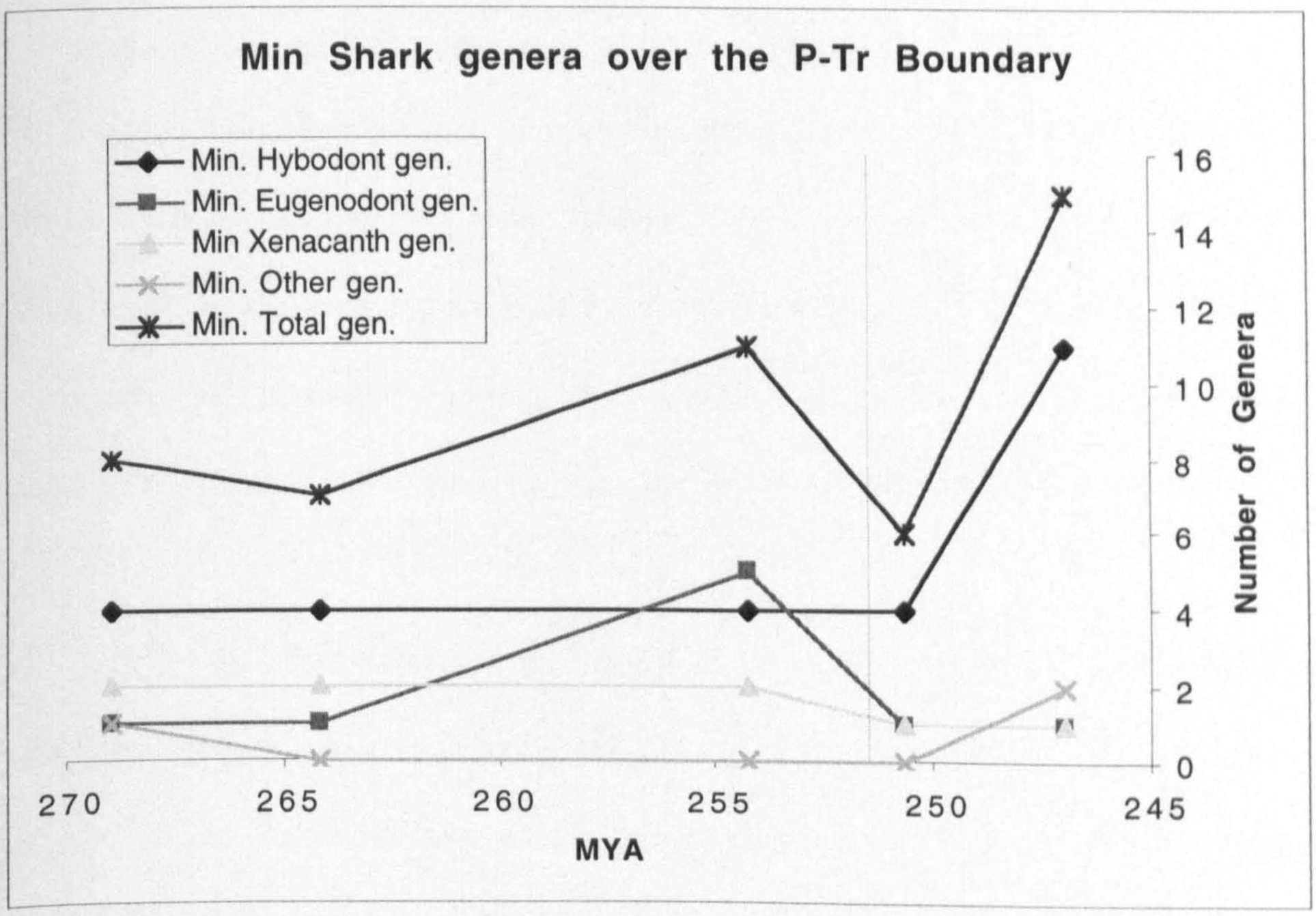


Fig. 3.3 Minimum Number of Shark genera over the P-Tr boundary

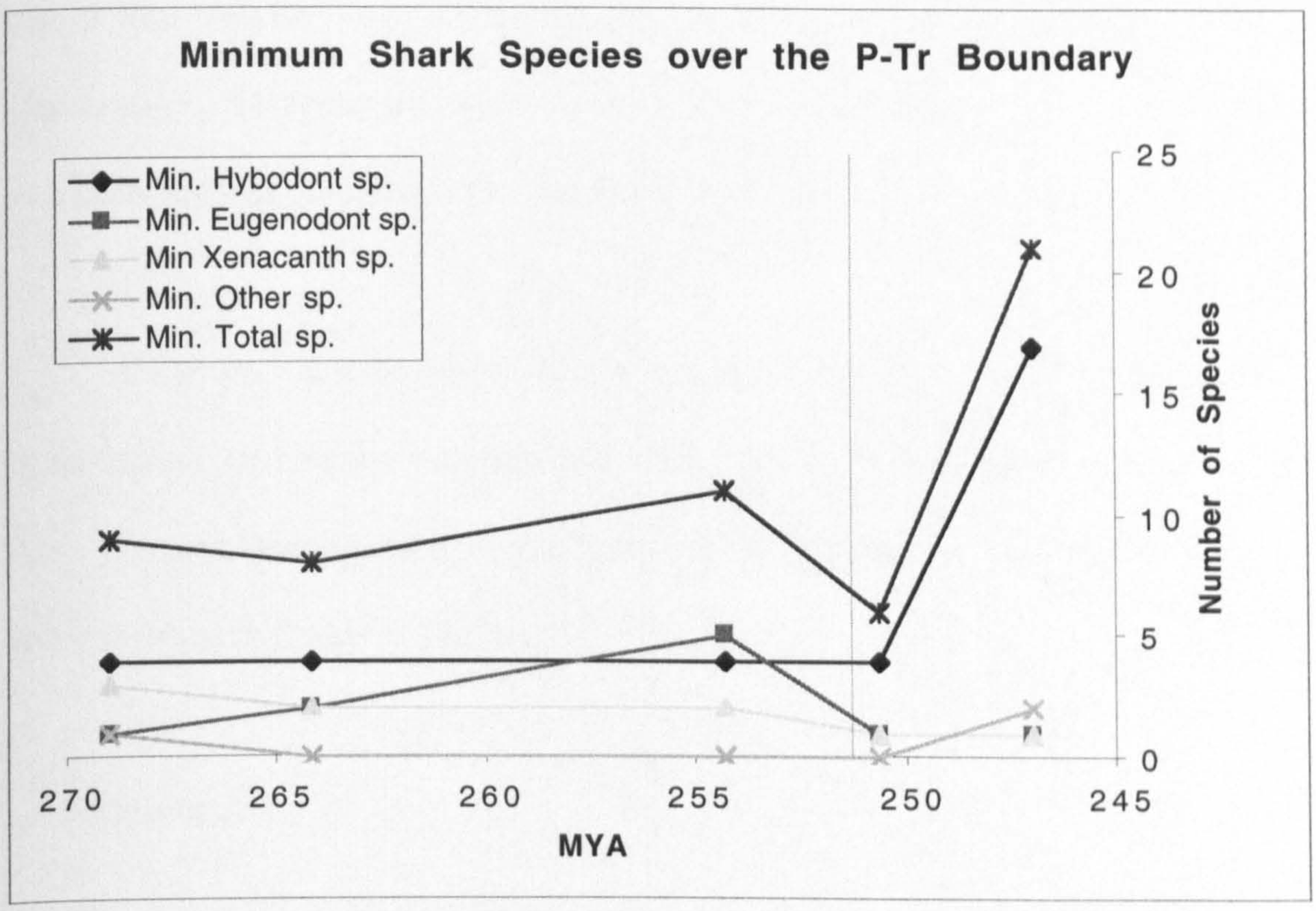


Fig. 3.4 Minimum number of Shark species over the P-Tr boundary

Wuchiapingian- Chanhsingian and hence their discovery from Russia would also not alter the diversity estimates. The acceptance of *Wodnika* sp. and *Palaeospinacidae* indet. would slightly increase the extinction estimate over the P-Tr boundary. Likewise the acceptance of *Hybodus zuodengensis* and *H. yohi* would slightly increase the diversification estimates in the Olenekian though these effects would be minimal.

If, in an effort to reduce the impact of lagerstatten effect on the visible pattern, only ghost ranges and specimens based exclusively on tooth data were considered the pattern would like wise not greatly alter. *Wodnika striatula* would no longer be considered in the Rodian but all species from the Wordian - Capitanian would still form part of the analysis. The data set from the Wuchiapingian – Changsingian would no longer include *Fadenia, Arctanacthus* and Hybodontiformes indet. The Triassic data set

would lose *Polyacrodus twitchetti* from the Induan while the Olenekian would lose *Wapitiodus* , *Lissodus* aff. *cassangensis* and *Palaeobates augustisimus*. While this obviously reduces the sample size the diversity pattern remains almost exactly the same.

If the data set were further altered to also remove ghost ranges the data set would be further reduced but the pattern would still remain the same i.e. relatively low diversity in the Permian, with a drop in diversity over the P-Tr boundary, followed by a rapid diversification in the early Triassic.

5.1.5 Conclusion

The data is too sparse to be statistically significant but there is anecdotal evidence to suggest some patterns. If it is assumed that, while the fossil record is less than complete, by using ghost ranges of genera found in the Lower Permian, most or all of the families and genera of sharks present in the Upper Permian have been accounted for, it can be seen from the above the survivorship of sharks over the P-Tr boundary is relatively high in comparison to the published figures for other groups. While the number of species that survived the P-Tr event is zero (a relatively common occurrence from one stage to another in sharks) the number of families that survive (71%) is far greater than seen in other published figures for the extinction. In addition to this, the rapid diversification of the surviving genera in the Olenekian shows that detrimental effects of the event on shark diversity where relatively short lived.

5.2 Effect of tooth morphology and likely diet on survival of sharks over the P-Tr boundary.

5.2.1 Introduction

Dentitions in modern sharks are separated into a number of categories. These include tearing, clutching, cutting, crushing, grinding and vestigal (Cappetta 1987)). Tearing teeth are usually high-crowned and extremely pointed, designed to pierce and hold active prey that are mainly fish. Clutching teeth are usually lower crowned and more robust and are designed to grasp shelled prey, this is a more generalised type of dentition. Cutting teeth generally have a sharp, usually serrated cutting blade designed to cut sections of flesh from relatively large prey. Crushing teeth are low and flat and are designed to feed on mainly hard shelled and relatively immobile prey. Grinding teeth compose a tooth pavement that can grind prey between the upper and lower batteries. Vestigal teeth are possessed by filter feeding sharks that retain small clutching type teeth but do not use them.

While it is clear that without direct evidence such as bite marks or stomach contents any statement about the diet of a fossil species is speculative, it is none the less possible to infer the general diet based on functional similarities with modern taxa. For ease of description in this work fossil shark dentitions will be limited to three types: piscivorous (similar to tearing and cutting teeth, i.e. feeding mainly on fish), generalist (similar to clutching, i.e. lower crowned and capable of feeding on both fish and soft shelled prey), durophagous (similar to crushing and grinding dentitions, i.e. feeding on hard-shelled prey).

Teeth from various shark groups show completely different shapes based on their origins and dietary function. Teeth from various parts of the dentition also have different morphologies. This is particularly obvious in the case of the eugeneodonts where the symphyseal tooth whorl is composed of teeth that have a totally different morphology than the lateral tooth pavement. If merely the shape of the symphyseal teeth were measured it could be concluded that eugeneodonts such as *Helicoprion* were piscivorous whereas examination of the tooth pavement clearly indicates a more durophagous diet. These factors make it difficult to find a common tooth measurement that would allow the definition of the various feeding groups. In addition to this very few papers list consistent tooth measurement, preventing the accurate comparison between sharks within the same group. So, measurements will not be used in determining the possible feeding methods, but rather a judgment will be made based on the overall morphology of individual teeth, reconstructions of dentitions and comparisons of both of these with extant sharks with known diets. When examining the change in feeding types over the P-Tr boundary only specimens that have been found will be incorporated. Genera assumed to be present due to ghost ranges will not be considered.

5.2.2 Permian

5.2.2.1 Roadian

The earliest shark finds from the Upper Permian come from the Roadian. A partial dentition of *Wodnika striatula* from Germany has been found and a number of

reconstructions have been attempted (Weigelt 1930, Schaumberg 1977). Schaumberg (1977) characterised the teeth as being "flat and bean shaped, unlike those of *Hybodus*" (*Hybodus* usually possessing high cusped piscivorous teeth). This would seem to indicate that *Wodnika* was a durophagous predator.

Two of the shark species from the U.S. (*Orthacanthus texensis* and *Orthacanthus platypternus*) are xenacanths and they share the usual three-pointed, cusp morphology, though the lateral cusps are slightly more robust and in the case of *O. texensis* are serrated. A number of people have speculated on the diet of these animals (Williams 1972, Johnson 1999). A number of prey species including amphibians and reptiles have been suggested, but the current consensus is that these animals would have had a piscivorous diet, i.e. feeding primarily on fish (Johnson 1999).

5.2.2.2 Wordian - Capitanian

The *Helicoprion* specimens from the Wordian-Capitanian of the USA (*H. ferrieri*, *H.* cf. *ferrieri*, *H. ergassaminon* and *H.* sp) are known almost entirely from isolated tooth whorls. These whorls are composed of lower symphyseal teeth that, instead of being shed, move forward, revolving into a circular shape that is housed in a cavity in the upper jaw when the mouth is closed. These teeth were usually fairly high crowned with serrated edges. Some other teeth, identified as anterior lateral teeth, have also been found in association with a partial neurocranium and are arranged roughly in rows. These teeth were described as low and rectangular with an upper crushing surface. If similar to other

eugeneodonts such as *Fadenia* these teeth would have formed a crushing tooth pavement making *Helicoprion* a durophagous predator.

The two Xenacanthidae indet. specimens (originally described as *Xenosynechodus*), found from Russia were originally described having teeth that are similar to those of *Synechodus* with a few differences keeping them from being assigned to the genus (Ivanov 2000). This would indicate teeth with high main cusps suitable for a piscivorous diet.

5.2.2.3 Wuchiapingian - Changhsingian

The next group of eugeneodonts are those from the Wuchiapingian of Greenland (*Sarcoprion edax, Fadenia crenulata* and *Erikodus groenlandicus*)

The symphyseal teeth in *Sarcoprion* are in both the upper and lower jaw and curved but do not form a spiral. They have a relatively high, serrated morphology indicative of a cutting function. The lateral teeth are small and morphologically fairly simple. *Sarcoprion* also has a pavement of parasymphyseal teeth. This would seem to indicate a generalist/durophagous predator.

Erikodus has the lowest crowned symphyseal with a rounded coronal surface. The lateral teeth are described as having a "serial arrangement" that again would be suited to a durophagous predator. The symphisial teeth in *Fadenia* are lower than those of *Sarcoprion* and have no serrations. The lateral teeth on both the upper and lower jaws are arranged into a crushing pavement suited to a durophagous diet

A specimen of *Helicoprion*, identified only as *H*. sp. was found in the Wuchiapingian of Japan. Though there is no actual description of this specimen illustrations indicate a tooth whorl similar in shape to than of the American *Helicoprion* species hence implying a durophagous predator. Another *Helicoprion* specimen was found from China though it is only described as being from the Upper Permian (Lei 1983).

The hybodont specimens from the Wuchiapingian – Changhsingian of the Vologda and Moscow districts in Russia, were originally described as *Polyacodus* sp. and *Lissodus bigibbus* . While there is no description for these teeth (preventing the acceptance of the taxonomic assignment) it is not unreasonable to assume that they have the same gross morphology as the genera that they were assigned to. *Polyacrodus* teeth are usually low-crowned and mesio-distally elongated with a low but still visible main cusp. This would allow feeding on a wide variety of prey species, making *Polyacrodus* a generalist predator. *Lissodus* has teeth with functional morphology similar to that of *Polyacrodus* i.e. a mesio-distally expanded crown with a low main cusp. It is therefore assumed that these unidentified hybodont specimens had a generalist diet.

The two specimens of *Helicampodus* from the Wuchiapingian – Changhsingian are *H. kokeni* was found from the Upper Permian of Pakistan and *H.* sp. from Japan. Zangerl (1981), described *Helicampodus kokeni* as having a symphyseal whorl similar to *Sarcoprion* which would indicate the genus had a generalist/durophagous dentition.

The only other durophagous shark found from the period was discovered in Russia and is herein referred to as Elasmobranchii *incertae cedis* (originally described as *Wodnika* sp., see chapter 4). Like the previously mentioned hybodont species from

Russia there is no available description to validate the generic assignment to *Wodnika* but it is assumed that the teeth have the same gross functional morphology and that therefore share the same durophagous feeding habits as the previously mentioned *Wodnika* species.

The only piscivorous shark species thus far known from the Wuchiapingian – Changhsingian was an *Orthacanthus* specimen from Japan. The specimen consists of a partial tooth composed of part of one of the two lateral cusps. The cusp is slender and curves to the inner or outer side one quarter of the way up its length. Each side of the cusp is serrated. When complete this tooth would have had the usual three cusped piscivorous morphology characteristic of xenacanths.

5.2.3 Triassic

Many of the Triassic specimens come from the same genera and as such have similar broad morphological features with small differences. These differences will be briefly mentioned but for a more in depth description of the taxa see chapter 4.0.

5.2.3.1 Induan

All the fossil sharks from the lowest Triassic (*Aconcinnodus claveringensis, Polyacrodus twitchettii, Lissodus angulatus* and *Parahelicampodus spaerki*) come from Greenland. *Aconcinnodus* is a new genus erected to accommodate some of the species previously assigned to *Polyacrodus* (Chapter 3.1). While the overall morphology of *Aconcinnodus* is different enough from *Polyacrodus,* the functional morphology is

largely the same with the teeth being mesio-distally elongated with a main cusp suited to a generalist feeding strategy. *Polyacrodus twitchettii* (for a detailed description see chapter 2.1) possessed teeth of the general *Polyacrodus* morphology previously described in addition to which it had relatively simple ornamentation and 1-2 pairs of lateral cusps. This morphology i.e. low and extended but with a main cusp would suggest an ability to feed on both hard and soft prey, i.e a generalist predator, though, its relatively small size would have precluded some of the larger prey items available. As well as the general characters attributed to *Lissodus*, *L. angulatus* has no or very poorly developed lateral cusps and very scarce (single vertical ridge) ornamentation. The feeding strategy in *L. angulatus* is likely to have been similar to that of other *Lissodus* and *Polyacrodus,* i.e generalist. The specimen of *L. angulatus* from Greenland was very small, limiting its possible prey, though larger teeth have been found (Duffin 1985). The only material of *Parahelicampodus spaerki* was a partial symphyseal series with no associated skeletal material or isolated teeth. The uppermost section of the symphyseal crowns is missing but the original reconstruction shows a relatively low and blunt crown (in comparison to other eugenodonts) ill suited to grasping fast moving prey such as fish. The lack of associated lateral teeth makes assignment of feeding type tenuous but if it did possess lateral crushing teeth normally associated with eugeneodonts, then *Parahelicampodus* could also have been a generalist predator.

5.2.3.2 Olenekian

There are two generalist species from the Olenekian of Canada. The specimens come from the Wapiti Lake area of British Columbia. There is a single specimen (isolated tooth) of a *Polyacrodus* species, though preservation is insufficient to identify it to species so it has been described as *Polyacrodus* sp. (Chapter 2.3.1). This specimen has the typical *Polyacrodus* tooth morphology suited to generalist feeding. The second generalist from the area is *Contrariodus*. Like *Aconcinnodus, Contrariodus* is a genus erected to accommodate species previously assigned to *Polyacrodus* (Chapter 3.1). The species found is *Contrariodus wapitiensis*. As could be expected from a genus that was previously described as *Polyacrodus*, *Contrariodus* has teeth suited for a generalist feeding strategy.

Several of the Olenekian species come from the already discussed *Lissodus*. These include *L. angulatus* form Spitzbergen, *L. cassangensis* from Angola, *L.* aff. *cassangensis* from Madagascar, *L. africanus,* the type species of *Lissodus,* from South Africa and *L. minimus* from Japan. All of these species share the general *Lissodus* characters with minor variations (for detailed descriptions see chapter 4.0) and would all have had the same general feeding strategy as the previously mentioned *Lissodus* species i.e. generalist predators.

Of the specimens found in the Olenekian of China, teeth assigned to *Polyacrodus tiandonensis* display the same gross morphology as the other *Polyacrodus* species described above and as such can be considered as a generalist.

In addition to the generalist feeders from Canada there is an undescribed species of eugeneodont from Wapiti Lake. No full description of the dentition is available as yet but the shark appears to have been similar in many ways to *Fadenia crenulata* from the Upper Permian of Greenland and therefore could have had a similar durophagous diet.

Other durophagous sharks found in the Olenekian include several species of *Acrodus*. These species include *Acrodus scaber, Acrodus spitzbergensis* and *Acrodus vermiformis* all from Spitzbergen as well as *Acrodus* sp. from Madagascar. The teeth in *Acrodus* sp. are low and flat and are ornamented by a series of fine bifurcating ridges. *Acrodus* has no obvious main cusp that could be used for grasping prey and instead has an almost exclusively crushing type dentition implying that it was a durophagous predator.

Palaeobates polaris, also from Spitzbergen, differed from other *Palaeobates* teeth in having anatomosing ridges originating from its occlusal crest forming a reticulated appearance. The teeth had a similar functional morphology to *Acrodus* teeth with a low rounded crown that was unsuited to grasping but constituted a more crushing dentition (Stensiö 1921) making it another durophagous predator.

The final species of *Palaeobates* from the Olenekian was *P. augustimus*, from Germany. *P. augustimus* also had teeth with a near-flat crown that would have formed a crushing durophagous dentition.

The only piscivorous shark to be found in Wapiti Lake is a previously undescribed hybodont named *Wapitiodus* (for full description see chapter 2.3.1). *Wapitiodus*, unlike the other genera from the area has high-crowned acuminate teeth

more suited for a piscivorous diet. It is also bigger than the other sharks from the area and would have been able to feed on the abundant teleosts also found from Wapiti Lake.

Three species of piscivorous sharks were also found in the Olenekian of Spitzbergen (*Hybodus rapax*, *H. sassienensis* and *H. microdus*). *Hybodus* teeth are characterised by a main cusp that is lengthened and pointed. This cusp that in many species is as high as the crown is long and is flanked on both sides by a number of lateral cusps (Agassiz 1837). This type of dentition would be ideal for grasping rapidly moving prey such as fish.

Synechodus sp. from Turkey, the earliest confirmed neoselachian find, had high crowned teeth suited for grasping, implying it also has a piscivorous diet.

Two species of ctenacanths were found from the Olenekian of China. While the generic assignment of these species may be in doubt (see chapter 4.0) the teeth have high accuminate cusps suitable for grasping implying a piscivorous diet.

5.2.3.1.1 Other Lower Triassic

There have been other teeth found in the Lower Triassic but no more accurate age is given, making accurate comparison difficult.

The description of *Helicampodus egloni* from the Lower Triassic of Armenia is, as previously stated, unavailable as is the description for the type species (*H. kokeni*) but Zangerl (1981) describes both of these species as having a symphyseal whorl similar to that of *Sarcoprion* which would imply a generalist/durophagous diet.

Acrodus substriatus from the Lower Triassic of India has teeth that have a long low crown with a slight elevation in the centre, but not enough to justify a main cusp. *A. substriatus* would have had the same durophagous dietary habits as other *Acrodus* species.

Triodus sp. from India has teeth that are slightly more robust than the previously described xenacanth teeth with main cusps that diverges slightly but the overall functional morphology is consistent with other xenacanths i.e. a piscivorous predator.

5.2.4 Discussion

As is the case in most aspects of studying the effect of the Permian mass extinction on sharks, there is a serious lack of material upon which to base any conclusions. This is especially true of the Upper Permian. Likewise the fossil record of the lowermost Triassic is very sparse with only four species from the Induan, and all of these from Greenland. There are far more species available for study from the Olenekian but faunas may already have recovered from any effects of the P-Tr extinction by then. The largest number of species within any one group at any one period never exceeds seven and this is generalists and durophages in the Olenekian. Despite the lack of data Chi squared analysis shows that there is a statistically significant link between feeding type over the P-Tr boundary.

Piscivory seems to be the least common of all the feeding types with 13 species from the study period utilising this feeding strategy, none Lowermost Triassic.

Durophagy is a more common feeding strategy with several durophagous sharks being found in the Upper Permian (one in the Roadian, four in the Wordian to the Capitanian and three in the Wuchiapingian). There are however no durophagous sharks from the uppermost Permian. There is a gradual increase in the number of generalist sharks from the Wuchiapingian to the Olenekian and only generalist feeders are found in the lowermost Triassic. The Olenekian sees the return of all three feeding strategies though generalism remains dominant.

It is not surprising that generalist feeders should be present in the Upper Permian and especially in the lowermost Triassic where a large number of prey species may have disappeared, leaving less specialised predators at an advantage. Other studies of species surviving the Permian mass extinction have shown that post-extinction communities are characterised by low diversity and complexity populated by simple ecological generalists (Schubert and Bottjer 1995). Schubert and Bottjer (2001) further stated that these post-extinction communities then remain dominated by generalist taxa until they are excluded by more specialised taxa returning from refugia. This would seem to hold true for shark faunas as, despite disappearing in the Induan, specialised taxa such as piscivorous xenacanths and durophagous eugeneodonts reappear in the Olenekian.

The lack of specialised predators such as piscivorous durophagous sharks does not seem unlikely following a major disturbance such as a mass extinction event. It does, however, seem strange that no durophagous sharks were found in the 3 million years

prior to the mass extinction event (all the Greenland durophagous eugeneodonts were found exclusively in the Wuchiapingian).

This lack of durophagous sharks could be due to the already mentioned poor Upper Permian fossil record or it is possible that an event prior to the P-Tr extinction event adversely affects this feeding group. There have been other studies suggesting an extinction event prior to the P-Tr mass extinction. Isozaki *et al.* (2004) identified two separate extinction horizons for the Upper Permian and Lower Triassic sequences at Chaotia in northern Sichuan, China. One of these extinctions was at the P-Tr boundary but the other was at the Guadalupian-Wuchiapingian boundary. There is, however, insufficient evidence to confirm this theory for the disappearance of feeding types in the Upper Permian. It seems more likely that the fossil record in the Upper Permian is simply incomplete.

One conclusion that can be drawn is that the presence of specialised taxa in the Olenekian indicates a relatively rapid recovery period for sharks following the P-Tr mass extinction. This is consistent with the data on shark size change over the P-Tr boundary.

5.3 Size change in sharks across the P-Tr boundary

5.3.1 Introduction

One of the many suggested consequences of the Permian mass extinctions is the so-called "Lilliput effect" (Urbanek 1993). The Lilliput effect manifests itself as a marked reduction in size of flora and fauna following a major disturbance event such as a mass extinction. It has been postulated that this reduction in size is as a result of a decline in primary productivity (Twitchett 2001).

There have been two major of theories to explain the cause of any observed size reduction during mass extinctions. The first was proposed by Twitchett (1998). He suggested that over the P-Tr boundary there was a major reduction in primary production. This was supported by a marine sequence deposited in a basinal setting at Williston Lake, north eastern British Columbia (Wang et al. 1994). The $\delta^{13}C$ values of kerogens in the rocks in this sequence show a shift at the Permo-Triassic boundary. This shift was explained by increased atmospheric CO_2 resulting in increased dissolved CO_2 due to reduced photosynthetic carbon use in the surface water. Twitchett further postulated that this reduction in primary production would have necessitated a reduction in biomass in all trophic levels that could have occurred in one of two ways. The first mechanism by which biomass could have been reduced would have been through a reduction in the body size of organisms while the second would have been a reduction in the number of organisms. A reduction in the size of organisms would have resulted in an obvious Lilliput effect while the reduction in number of organisms would have resulted in

increased apparent extinction of larger organisms due to reduced preservation potential, hence also resulting in a lower mean body size within groups (Twitchett 1998).

The other potential cause of size reduction during mass extinction events is the "life history strategies" used by various groups (De Blanger 2001). Most organisms employ, to a greater or lesser degree, one of two life history strategies dubbed r or K (MacArthur and Wilson 1967). Organisms that use r life history strategies are usually small, fast growing, widely dispersing species with very rapid turnover rates. K selecting species on the other hand are large, slow growing localised species that have very low turnover rates but tend, in the long term, to out compete r selecting organisms. This r and K selection in also observable in the fossil record. Larger-bodied organisms that occupy stable environments have a reduced probability of extinction, in normal times, in comparison that species that inhabited less stable shallow seas (Ward and Signor 1983). In times of mass extinction smaller organisms that inhabit less stable environments fare better (Jablonski 1986, Hallam 1987, Chiba 1998). Thus in times of mass extinction small species would survive preferentially to large species causing a mean size reduction.

While the ultimate result of both reduction in primary productivity and selection based on life history strategies would be the same, i.e. mean size reduction of organisms, the speed and victims of the events could be different. In the case of primary productivity decline causing reduction in body size you would expect there to be a gradual reduction in size with the organism diversity remaining the same. However both reduction in biomass by reduced population size and preferential survival due to r-selection would be more rapid and would result in either the real or apparent extinction of several groups. It

may however be possible to distinguish between real and apparent extinction if later Lazarus taxa are discovered.

Several studies have been carried out examining the extent of the Lilliput effect on post-Permian communities with varying results. Most of these studies have concentrated on groups with relatively rapid reproductive cycles from low trophic levels. As yet there has been no serious study on the extent of the Lilliput effect on top predators with relatively long reproductive cycles such as sharks. This work aims to fill that gap.

In order to measure any possible difference in size between the pre- and post-mass extinction fauna it is necessary to gather as many specimens as possible that could be used to give an indication of the shark's original size. Isolated teeth are obviously not suitable for this as sharks shed several thousand in their lifetimes and the relative size of teeth can vary greatly from shark to shark depending on its feeding strategy. To this end I have attempted to gather as many body fossils as possible from the Upper Permian and Lower Triassic and compared them with typical shark reconstructions to allow an estimate of size to be made. The standard reconstruction used for hybodonts was that of Maisey (1982) which was based on parts from several hybodonts including *Hybodus basanus, H. hauffianus, H. fraasi* and *Lissodus cassangensis*. The eugeneodonts were compared to either known specimens of their own genus or in the case of the undescribed Wapiti Lake sharks to the eugeneodont genus them most resembled, usually the reconstruction of *Fadenia crenulata* made by Nielsen (1952). While the Wapiti Lake specimens have not been described in this work they are listed with very brief descriptions in order to increase the available sample size. In order to get size estimates the preserved sections of the various specimens were compared to the reconstructions

mentioned above and the ratio of the specimens/reconstruction was multiplied by the size estimate for the reconstruction.

Several problems come to light when comparing the change in body size over the P-Tr boundary, most resulting from the poor preservation potential of cartilaginous fish and the subsequently incomplete fossil record. There are very few specimens in the Upper Permian that can be used to estimate the size of the sharks around during the period. With almost no specimens comprising postcranial elements. In the case of some Permian eugeneodonts (*Helicoprion*) size estimates have been made on tooth whorls as these are more indicative of size than isolated teeth and are necessary in order to bring the sample size up to a realistic level for even the most basic comparison. There are ten described *Helicoprion* specimens from the Upper Permian. Most of these are specimens of *Helicoprion ferrieri* (Idaho, USA) but there are also single specimens of *H. eragassamion* and *H.* sp. (both also Idaho, USA). No body fossil of *Helicoprion* has ever been found, making an accurate estimate of size impossible. Many workers have estimated the size of *Helicoprion* as being in the region of 2 m (Gilles Cuny pers. comm. 2004) but this can only be considered as a very rough estimate. The only specimen that has anything other than teeth preserved is a specimen of *H. ferrieri* (Bendix-Almgreen 1966) that has fragmented sections of the anterior neurocranium. Comparison of the most complete *H. ferrrieri* specimen with specimens of the most completely known Permian eugeneodont (i.e. *Fadenia*), then subsequent comparison of all other *Helicoprion* specimens to this, will allow for slightly more accurate estimates. When estimating the size of *Helicoprion* specimens it is assumed that the size of the skull is directly

proportional to the size of the tooth whirl. These size estimates will still however be subjective and useful only for broad scale size change analysis.

The Upper Permian record of hybodont body fossils is next to non-existent with only a few *Arctacanthus* cephalic spines available to allow very rough estimate of body size. Estimates based on these are possibly the most tenuous as there are no other hybodont cephalic spines that closely resemble them in morphology. Most other hybodont cephalic spines are more robust and have a relatively broader base. This scarcity of sharks in the Upper Permian could be representative of a real lack of diversity possibly due to an earlier extinction event at the base of the Wuchiapingian (Stanley and Yang 1994). It could equally be due to an incomplete fossil record caused by a mixture of a lack of shark bearing Upper Permian outcrops and the poor preservational potential of cartilaginous fish. In either case it makes a representative estimate of shark size very difficult.

The Lower Triassic is better, with 29 specimens on which body size estimate can be made yet there are still problems. Most of the Lower Triassic specimens come from the same locality (Wapiti Lake) making the sample distribution unrepresentative. In addition to this, most of the specimens are Olenekian or younger, with only three being found from lower in the Triassic (and all of them from Greenland). While less than perfect, this is still 22 more specimens than were previously available for study and as such a vastly more representative sample than was ever previously possible. A final problem when considering any patterns drawn from this data is that almost all of the specimens upon which a sizes estimates are being made are from different species. As a result of this making an estimate of error in any of the size estimates is impossible. While

not perfect, the sample can still be use to gauge a rough idea of possible size change and the large number of Olenekian specimens can be used to see, if sharks did experience a Lilliput effect over the P-Tr boundary, how long it persisted.

5.3.2 Upper Permian

5.3.2.1 Hybodonts

Specimens of hybodonts from the Upper Permian that consist of more than just isolated teeth are limited to two cephalic spines from Greenland assigned to the genus *Arctacanthus*. Size estimates, based on other hybodont spines of similar length (though quite different morphology), place *Arctacanthus* at between 1 and 1.3 m

5.3.2.2 Eugeneodonts

The second group of Upper Permian sharks are the *Helicoprion* specimens that come from the Wordian to the Capitanian of Idaho, USA. Of the ten specimen of *Helicoprion* from Idaho only six can be used for size estimates as the others have either no published size data or are too fragmentary to yield useful information. Of the remaining six specimens, five are examples of *Helicoprion ferrieri*. The *H. ferrieri* specimens would have been (from largest to smallest) 1.4, 1.27, 1.2, 0.8 and 0.48 m long respectively. The final Idaho specimen is an example of *H. eragasmion* that would have

been 1.23 m in length. Previous size estimates for other *Helicoprion* specimens have been in the region of 2m.

The other major group of eugeneodonts come from the uppermost Permian of Greenland, and they are split into three genera. Each genus is represented by several specimens, but due to ongoing cataloguing, several specimens are unaccounted for. For this reason one size estimate will be given for the genus as a whole, based on the most complete material as opposed to each individual specimen. The size estimate for *Fadenia* is based on portions of the tooth whirl, neurocranium, branchial arches pectoral, dorsal and caudal fins. In life *Fadenia* would have been roughly 2 m in length. *Sarcoprion* is less well known and size estimates for this are based only on the tooth whirl and sections of the neurocanium. *Sarcoprion* would have been the largest of the Greenland eugeneodont in the region of 2.2 m. *Erikodus* is the smallest and most incompletely known being based on only a tooth whirl. *Erikodus* would have been in the region of 1.5 m long.

5.3.3 Lower Triassic

5.3.3.1 Hybodonts

All body fossils from the Induan are hybodonts and come from Greenland . The first is a partial neurocranium, jaw and branchial arches that come from a specimen of *Lissodus angulatus*. The size of the fossil indicates a shark that would have been 11 cm in length. *Lissodus* species are always small in comparison to other hybodonts but this one

is particularly so. The second specimen from the Induan of Greenland is an almost complete body of *Polyacrodus twitchetti*. This specimen consists of a cranium, pectoral fins, both dorsal fins and a partial vertebral column but is missing the anal and caudal fins. The preserved section indicates a shark that would have been roughly 20 cm long. The final specimen consists of a jaw and branchial arches and has also been identified as *Polyacrodus*, although no teeth have been recovered from it. This specimen would have been 81 cm long in life. It is impossible to gauge how small these are for *Polyacrodus* specimens as they are the first body fossils to have been found but there have been teeth found from other *Polyacrodus* specimens that are far larger.

The Olenekian has a much greater wealth of hybodont skeletal finds, with 17 specimens coming from several different localities. The most abundant fossil finds come from the Wapiti Lake region of British Columbia (Canada). This area has yielded ten specimens from which size can be estimated. These specimens come from three different identifiable genera with one specimen coming from an *incertae sedis*. The first specimen described from the area was assigned to *Palaeobates* by Schaeffer and Magnus (1972), though no teeth were found to confirm this identification. This specimen was a partial head and body, though it lacks the anterior portion of the skull and the two dorsal fins. The original shark would have been 110 cm in length. *Palaeobates* is known from other skeletal material in the middle Triassic of Spitsbergen. The Spitsbergen specimen would only have been roughly 90 cm in length making the Wapiti specimen large in comparison.

The largest and most complete specimen of *Wapitiodus* from the area is located in the Royal Tyrrell Museum of Palaeontology and is an almost complete body with just a

section of vertebral column and the caudal fin missing. When complete this specimen would have been approximately 79 cm in length. The remaining two specimens of *Wapitiodus* are both located in the University of Alberta collections. The first is a section of vertebral column and an anterior dorsal fin from a specimen that would have originally been 97 cm long. The second is much smaller and is composed of the anterior 4/5 of the body with the posterior section of the caudal fin being missing. This specimen would have been roughly 26 cm in length. This may have been a juvenile but preservation is insufficient to make out much detail of the clasper complex so this is impossible to determine.

Contrariodus is represented by four specimens from Canada. The first of these specimens (UAE 46527) is a partially preserved vertebral column with both dorsal fins. When alive the shark would have been roughly 85 cm long. The second specimen (UAE 46528) is less complete and consists of only a section of vertebral column and the anterior dorsal fin. This specimen would have almost exactly the same size as the previous *Contraridous* at approximately 85cm in length. The third *Contrariodus* specimen is a caudal fin that would have come from a 65 cm long shark. The most complete, and smallest of these specimens consists of the anterior 2/3 of the body, missing just the extreme posterior portion including the caudal fin. The specimen would only have been 32 cm long.

The final hybodont specimen from the Wapiti Lake area is a caudal fin, vertebral column and a partially preserved posterior dorsal finspine. The specimen (tmp 83.205.62) would have been 113 cm when completed making it the largest specimen found from the Wapiti Lake area.

The second largest repository of Olenekian shark specimens comes from sites in Northern Madagascar. Madagascar has yielded 5 specimens that can be used for size comparisons. The first specimen from this area is assigned to *Acrodus*. This specimen consisted of a portion of the cranium as well as the upper and lower jaws. The shark would have been 137 cm in length when alive. *Acrodus* is based largely on teeth with a few spines also having been found. *Acrodus* was a relatively large hybodont with the size displayed from the Madagascar specimen not being unusual for the genus.

Three of the remaining four specimens from Madagascar are from the genus *Lissodus*. These specimens vary in their completeness. The most complete consists of most of the anterior body but is missing the rear section (from just anterior to the posterior finspine) including the pelvic, anal and caudal fins. The specimen would originally have been 16 cm long. The second specimen has virtually the same sections preserved but is slightly smaller and would only have been 14 cm long. The final *Lissodus* specimen is seen in dorsal view and consists of a partially preserved neurocranium, vertebral column and dorsal finspines. This specimen would have been the smallest at 12 cm in length. The only other hybodont specimen from Madagascar, classified as Hybodontiformes indet, is a pelvic fin (described in this work) that would have belonged to a 56 cm long shark.

The final Lower Triassic hybodont specimens are also from Africa, two from Angola and a number from South Africa. The two specimens from Angola (one male and one female) are from the Olenekian and have both been assigned to *Lissodus cassangensis*. They are both preserved from just posterior to the head region to just anterior of the caudal fin. Both specimens would have been roughly 20 cm in length i.e.

significantly larger than the *Lissodus angulatus* specimen from the Lowest Triassic of Greenland.

The final locality that has thus far yielded Lower Triassic hybodont body fossils is Bekker's Kraal South Africa. This site has yielded several specimens of *Lissodus africanus*, the type species of *Lissodus*. While the site has yielded in excess of 20 specimens size data on most appears to be unavailable. According to Brough (1935) the mean size appears to be 20-25 cm with one specimen possibly exceeding 40-45 cm. These specimens are also clearly greater in size than the Greenland *Lissodus* specimen.

5.3.3.2 Eugeneodonts

In addition to the wealth of hybodont specimens found there, Wapiti Lake has also yielded several eugeneodont specimens that can be used for size comparisons. The eugeneodonts originally found from the Wapiti lake area where preliminarily assigned to *Edestodus* (Neuman 1992) but these, and newly found specimens are currently undergoing re-description by Raoul Mutter. Given the lack of accurate taxonomic classification it is impossible to tell whether these sharks are small representatives of their genera and can only be compared to the eugeneodont group as a whole.

There are 11 eugeneodont specimens from the Wapiti Lake that can be used to get an estimate of body size. There are a number of other specimens but they are too fragmentary to be truly useful. The first group of specimens are from the University of Edmonton collection and are in order of specimen number. Specimen UAE 17928 is a dorsal fin that measures 12 cm in height. This original shark would have been

approximately 120 cm in length. Specimen UAE 19729 is a partial caudal fin that would have come from a shark that was roughly 80 cm long. Specimen UAE 36536 is a partially preserved scapulacoracoid and pectoral fin. In life the specimen would have measured roughly 130 cm.

Specimen tmp 86.42.04 is a fairly well preserved anterior body section (to just posterior of the pectoral fins) that measures 28.5 cm in length and would have come from a 70 cm long shark. Specimen tmp 86.42.04.2 is a caudal fin and posterior body section that was thought to be part of the previously mentioned anterior body section, though this now seems unlikely. It would originally have come from a 98 cm long shark. Specimen tmp 87.42.8 and tmp 87.42.9 are both pectoral fins and would have come from 110 cm and 90 cm long sharks respectively. Parts of the anterior body as well as a pectoral fin are preserved in specimen tmp 87.42.11 with the animal originally having been 70 cm in length. Specimen tmp 88.98.92 is an anterior body section (posterior half of the head to roughly 1/2 of total body length) from an unusually small eugeneodont that would only have been roughly 18 cm long. It is possible that this specimen may have been a juvenile. Specimen tmp 95.118.1 is another pectoral fin and body section that would have come from a 55 cm long shark and the final Wapiti eugeneodont specimen is a partial caudal fin from a 82 cm animal.

5.3.4 Discussion

The size distribution of all shark specimens described above is plotted in Fig. 3.4. When the estimate of the body sizes of all sharks found over the study period was subjected to analysis of variance for statistical significance it was shown that, at the 95% level, there is a very significant difference over the p-Tr boundary. When viewed as a whole, the mean size of sharks follows a pattern (Fig. 3.5) of slight increase in size during the Upper Permian from 80 cm to 175 cm, followed by a reduction over the P-Tr boundary to 37 cm, and then an increase over the Lower Triassic to 77 cm. This shows an overall reduction in the mean size of sharks of 79% over the P-Tr boundary.

The statistical significance of hybodont body size is not as extreme as for all sharks as a whole but is never the less significant. The hybodont size distribution pattern appears to show an increase in maximum size during the Upper Permian from 80 cm to 130 cm followed by a drop in maximum size over the P-Tr boundary to 81cm (38% decrease) and then an increase between the Induan and the Olenekian to pre-extinction sizes. The mean size change pattern is similar with a reduction from 130 cm to 37 cm (72% decrease) over the P-Tr boundary followed by an increase to pre extinction levels. This is however a tenuous pattern as the entire Upper Permian record consists of only two specimens and the lowest Triassic only has three specimens. The Olenekian sample is slightly more representative with 16 specimens. This sample size is insufficient to state with certainty that there was a definite size reduction in hybodonts over the P-Tr boundary. The presence of hybodonts in the Olenekian, that are as large as pre-extinction

specimens, does however allow for the conclusion that any effect of the extinction event on the size of hybodonts was short lived.

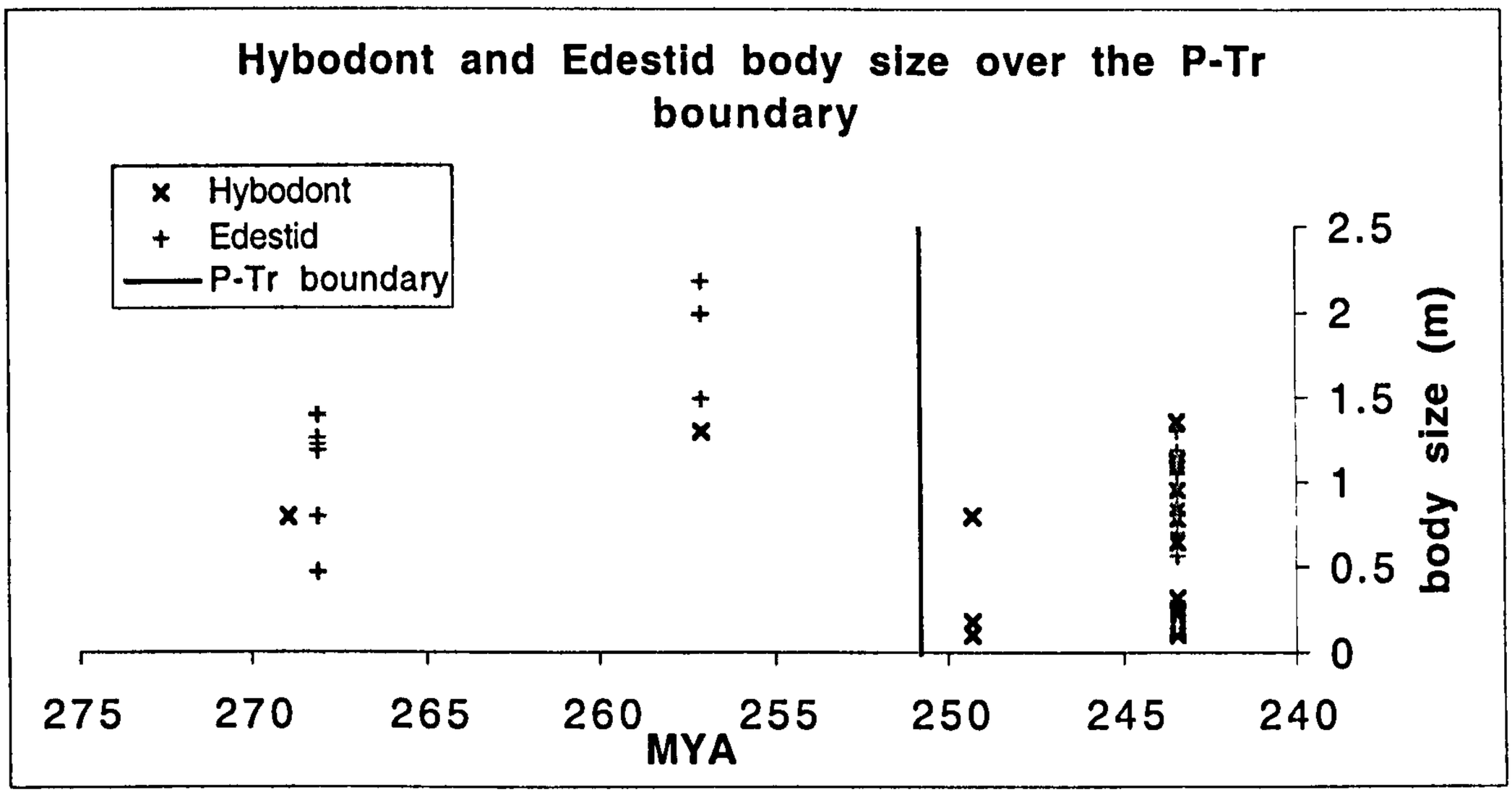


Fig 3.5. Shark size distribution over the P-Tr boundary

The estimate for statistical significance of the eugeneodont over the P-Tr boundary are not significant at the 95% level thought this likely due to the complete lack of fossil finds in the lowest Triassic. Despite the lack of statistical significance the following patterns can be seen. There are nine size estimates for eugeneodonts in the Upper Permian and 11 in the Lower Triassic, though none in the Lowest Triassic. Eugeneodonts also show an increase in size over the Upper Permian from 127 cm (max) and 106 cm (mean) to 220 cm (max) and 190 cm (mean). While there are no eugeneodont remains in the Induan that would allow an estimate of size to be made it is still possible to infer a reduction in size over the P-Tr boundary due to the number of relatively smaller eugeneodont found in the Olenekian of Canada. The largest eugeneodont from is 130 cm with the mean being 86 cm. This represents a maximum and mean size decrease of 41%

and 55% respectively. Eugeneodonts clearly did not return to pre-extinction sizes as quickly as hybodonts though why this could be is unclear.

The most obvious potential bias in the analysis of the available data on body size is that the specimens analysed may be from several different ontogenetic stages. If some of the specimens were fully grown, mature sharks while others are merely juveniles it could create an artificial size change pattern. Most of the specimens are far too poorly preserved to accurately determine ontogenetic stage and so the only way to limit the effects of this bias is to consider only maximum body sizes. As previously stated the hybodont specimens show an increase in maximum size during the Upper Permian from 80 cm to 130 cm followed by a drop over the P-Tr boundary to 81cm (38% decrease) and then an increase between the Induan and the Olenekian to pre-extinction sizes. The eugeneodont pattern is similar with a rise in maximum size over the Permian from 127 cm to 220 cm followed by a reduction in from the Upper Permian to the Olenekian to 130 cm. The difference in size variation is not as extreme when considering only maximum sizes but it still shows the same pattern and when all samples are considered.

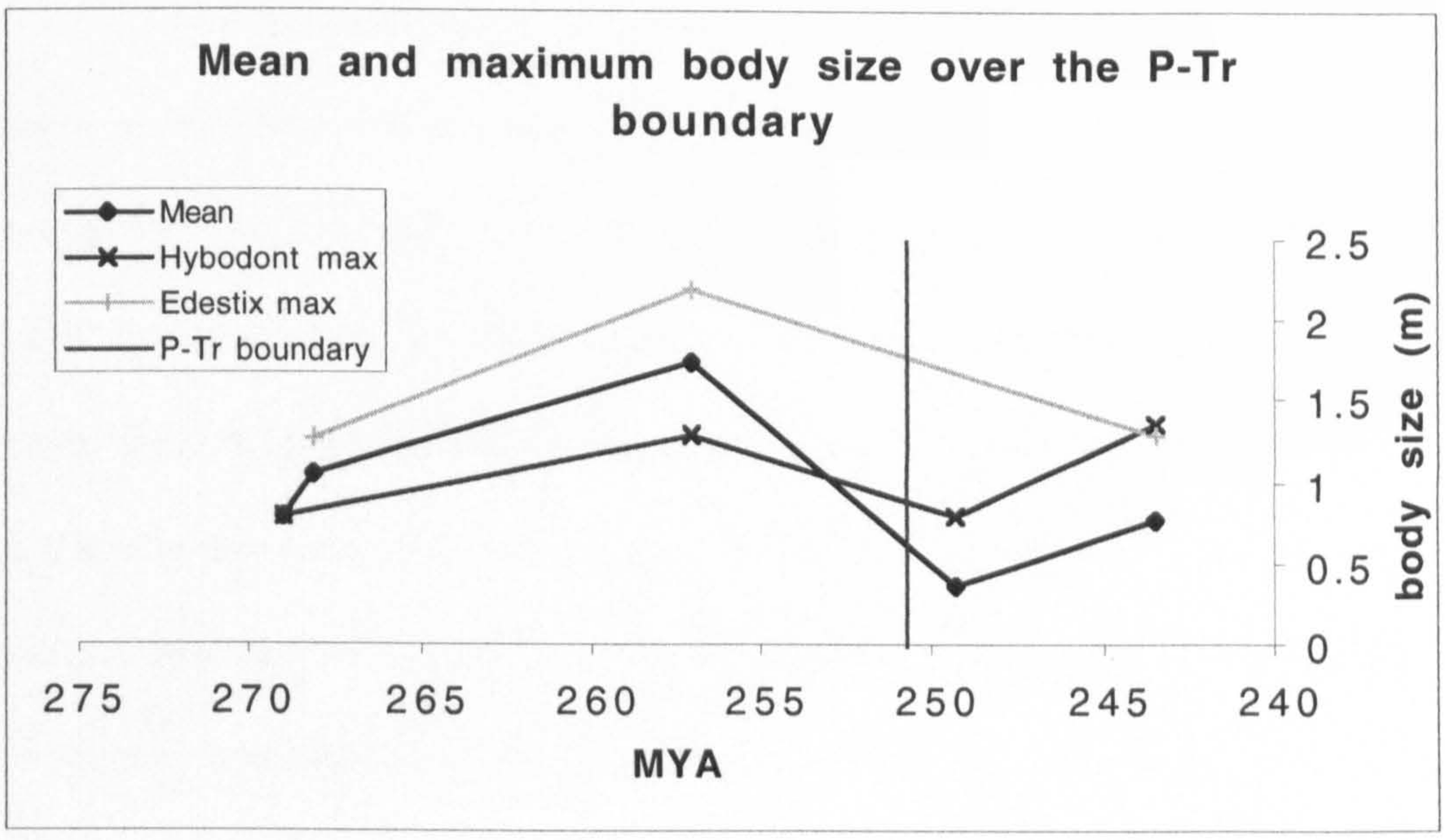


Fig. 3.6. Mean and maximum distribution of shark body sizes over the P-Tr boundary

This pattern is similar to other published observations of the Lilliput Effect, though quantitative evidence over the P-Tr boundary is actually fairly limited, although there are studies in preparation (R. Twitchett pers. comm. 2004). There have been a number of studies that present anecdotal evidence of slight body size reductions over the P-Tr as well as other extinction events. Faunal groups for which anecdotal evidence exists include conodonts over the P-Tr (Kozer 1996), corals S-D (Kaljo 1996) and there is some evidence of size reduction in trace fossils P-Tr (Twitchett 1999). There is some quantitative evidence of a roughly 40% size reduction in conodonts over the D-C (Girard and Renaud 1996). The only quantitative study of size reduction that has been published about the P-Tr boundary was by Price-Lloyd and Twitchett (2002) and shows between a 65 and 75% size reduction in molluscs. There are however other studies on K-T bivalves (McClure and Bohonak 1995), showing that size has no effect on survivorship of mass extinction events.

If we assume that the observed pattern, however statistically tenuous in some cases, is real then it can be seen that sharks suffer an extreme size reduction over the P-Tr boundary. This size reduction is as high if not higher than published information for any other group affected by the extinction event. It is not entirely surprising that sharks experience a large reduction in size as the higher trophic levels in any food chain, especially those dominated by highly specialised predators, are usually the least stable (MacArthur and Wilson 1967). Compared to other groups studied, sharks were high-level predators with relatively long reproductive cycles and hence clearly had more K orientated life history strategies. There is still, however, some evidence of variation in life history strategies in sharks derived mainly from extant species. Several recent studies have been performed on modern sharks to determine their rebound potentials from various forms of disturbance (Smith, Au and Show 1998; Frisk, Miller and Fogarty 2001). These studies examined the intrinsic rebound potentials of 26 species of Pacific sharks. It was discovered that rebound potential was strongly correlated with age at maturity (with the fastest maturing species having higher rebound potentials) but not with maximum age. As a rule the smaller-sized species tended to mature earlier, be shorter lived and have higher intrinsic rates of increase than larger species as is expected from the r and K selection theory. The studies found that sharks with the highest rebound potentials were smaller inshore short-lived species such as smoothhounds and sharpnose sharks. It was hypothesised that the small size of these sharks might have made them more prone to predation and hence they evolved a rapid turnover and maturation rate to increase the likelihood that their offspring would reach maturity and begin reproducing.

Small Palaeozoic shark species may have experienced similar selection pressures and evolved r-type life history strategies accordingly.

If similar to modern sharks of comparable size, the long reproductive cycle of large species would have made the slow reduction of body size due to a reduction in primary production unlikely. It is far more likely that larger sharks would have simply died out to leave the smaller species to survive and diversify.

This may also explain why, even though they cross the boundary and survive into the Lower Triassic, eugeneodonts do not regain their pre-extinction body sizes and disappear after the Olenekian. Permian eugeneodonts were far bigger and more specialised predators than hybodonts at the time and following the end-Permian event, the smaller and more generalised hybodont survivors experienced a massive diversification to well above pre-extinction levels while eugeneodonts failed to recover and eventually became extinct.

In conclusion, it can be seen that, the available evidence suggests that sharks did undergo a substantial reduction in body size from the Permian to the Triassic. The maximum size of hybodonts reduced by 18% while the mean reduced by 72%. Eugeneodonts suffered a reduction in maximum size of 41% and mean size reduction of 55%. Hybodonts however returned to pre-extinction sizes by the Olenekian while eugeneodonts remained smaller in the Olenekian and became extinct immediately thereafter. This difference in recovery pattern may have been due to the higher rebound potential of the smaller sized more generalised hybodonts.

5.4 Preferential survival of sharks in marine vs. freshwater environments over the P-Tr boundary

5.4.1 Introduction

In terms of palaeoenvironmental tolerances over the Permian and Triassic, sharks can be considered to fall into one of three groups. There are shark groups that thus far are believed to be exclusively freshwater. These sharks are predominantly xenacanths, traditionally viewed as most prolific in the Carboniferous and Lower Permian, faring badly in the P-Tr extinction event. Secondly there are sharks that have been found exclusively in marine conditions. These include eugeneodonts, that are also generally considered to be Palaeozoic fish and some hybodonts such as *Acrodus*. Finally there are shark groups that have been found in both marine and freshwater conditions. These are mostly hybodonts such as *Lissodus, Polyacrodus* and *Hybodus* but also include enigmatic genera such as *Wodnika*. Hybodonts are generally considered as a Mesozoic fish group that diversified in the Triassic and remained relatively abundant until their eventual extinction in the end-Cretaceous event.

The extent of the effects of mass extinction events on groups from varying aquatic ecosystems is a subject on which there has been relatively little work. There are some references to extinction events such as the Late Devonian mass extinction having less effect on freshwater than marine communities (McGhee 1996) but there appears to be little data on the subject. Padian and Clements (1985) suggested freshwater fish and amphibians where less affected less than their marine counterparts and that sharks, being a predominately marine group suffered relatively more in the P-Tr event. By examining

the environments from which all upper Permian and Lower Triassic sharks have been found this chapter aims to discover if freshwater sharks did indeed survive preferentially to those found in marine environments.

5.4.2 Permian

5.4.2.1 Marine

The vast majority of the shark finds in the Permian were marine in origin. Though few papers go into detailed specifics of palaeoenvironments, it is likely that most sections are coastal or shallow shelf. Each shark fauna will be briefly mentioned (for more detailed descriptions see chapter 4) and, where available, more accurate environmental settings will be stated. The two species of *Orthacanthus* from the USA were found from a coastal marine section (Johnsson 1999) whereas the larger *Helicoprion* species (Bendix Almgreen 1966) would have come from a deeper shelf environment. The palaeoenvironmental setting from which the Greenland eugeneodonts (*Sarcoprion, Erikodus and Fadenia*) and the hybodont *Arctacanthus* originated was a 400 km wide, cool water (35°N) embayment (Temmerik *et al.* 2001). The *Wodnika* specimens from Germany come from a shallow coastal shelf setting (Holzapfel and Malzahn 1984). The *Helicampodus* specimen from Pakistan comes from the *Productus* limestones of the Upper Permian indicating a clear marine origin. The *Helicoprion* specimen from China has no specific environmental information but the presence of various associated fauna used to date the find implies a marine environment. Finally the shark faunas from Japan

(*Helicoprion*, *Helicampodus* and *Orthacanthus*) also lack any detailed palaeoenvironmental information but it is likely that *Orthacanthus* inhabited a shallow shelf environment while the two edestids would have come from a deeper shelf setting as in the USA.

5.4.2.2 Freshwater

The only countries where Upper Permian freshwater sharks have been discovered are Russia and Brazil. The specimen found from Brazil comes from a continental section from the Rio do Rasto Formation. The specimen consists of a single isolated fin spine, which is only described as Hybodontiformes indet.

There is more material from the Upper Permian of Russia but there is still relatively little available information or descriptive data concerning the material. All the systematic assignments are based on either fin spines (which are not diagnostic) or poorly preserved teeth and in many cases the specimens are not described beyond the generic level. This brings the validity of the original generic assignments into question (see chapter 4). All of the specimens (previously described as *Wodnika, Xenosynechodus, Lissodus* and *Polyacrodus*) come from continental freshwater sections in the East European Urals area. The stratigraphy of the area is described in Newell *et al.* (1999) and Tverdokhrebov *et al* (2005). The presence of a xenacanth specimen (Xenacanthidae indet) is not unusual as they have been found predominantly in freshwater habitats. The presence of the hybodonts is also not overly unusal. While hybodonts are less frequently found in freshwater than xenacanths it is not uncommon. Hybodont genera such as

Lissodus have previously been found in freshwater (including the type species, *Lissodus africanus* (Broom). Without further study of the original material little can be said about the specimen of Elasmobranchii *incretae cedis*

5.4.3 Triassic

5.4.3.1 Marine

As previously stated, the only shark finds from the Lowest Triassic (Induan) come from Greenland. In the lowest Triassic Greenland was a shallow (50 to 100 m) marine shelf with a variety of depositional environments.

There were far more shark finds in the Olenekian most of which were also marine. Three hybodont genera (*Polyacrodus,Wapitiodus* and *Contrariodus*) as well as a thus far undescribed edestid genus were found in the Wapiti Lake area of Canada. In the Olenekian this area was a "relatively shallow-water, deltaic to shallow continental shelf environment, in an initially transgressive (Phroso-like strata), but subsequently regressive (Vega-like strata), sea influenced by turbidity and/or storm generated currents." (Neuman 1992). The hybodont genera from Spitzbergen (*Hybodus, Acrodus, Lissodus* and *Palaeobates*) as well as the unnamed edestid came from a sublittoral to shallow nerktic zone with the depth of this basinal setting within the range of the wave base (Birkenmajer and Jermanska 1979). The *Palaeobates* specimen from the Olenekian of Germany was found in a marine setting caused by a temporary marine influx of an otherwise continental area of Rhenish Bavaria during the Upper Bunter (slab sandstone). No

palaeoenvironmental information is included with the description of the earliest confirmed neoselachian tooth (*Synechodus* sp.) from Turkey but it was found with the conodont *Neospathodus cristigall. Neospathodus* has previously been found in basinal, inner and outer shelf environments (Carr *et al* 1984). The marine sharks from Madagascar (*Lissodus, Acrodus*, Hybodontiformes indet) come from an epicontinental warm and shallow sea setting with a depth of 200-300 m (Beltan 1996). The shark taxa from the Olenekian of India (*Triodus* and *Acrodus*) come from the marine *Otoceras* zone, though there is little detailed information about the palaeoenvironment. There is no available strategraphic information beyond marine for the eugeneodont shark (*Helicampodus elgoni*) from the Lower Triassic of Armenia. Lower Triassic marine sharks from Japan are limited to a number of isolated teeth and dermal denticles (Goto *et al.* 1996) found from the Grey limestone of the Taho Formation which occurs as an exotic block in Jurassic rocks. The unit is composed of biomicrite including abundant thin-shelled bivalves. Therefore, the Taho Limestone was probably deposited on a seamount (Koike,1994). China has also yielded shark teeth, though the generic assignment of these is also somewhat suspect. Wang *et al.* (2001) described a shark fauna consisting of two Ctenacanth specimens and a single species of *Polyacrodus*.

5.4.3.2 Freshwater

There are no freshwater sharks found in the Lowest Triassic. The earliest occurrence of a Lower Triassic freshwater shark is in the Olenekian where they are found from three countries (South Africa, Angola and Russia). Two of the Lower Triassic

freshwater shark species have been assigned to the genus *Lissodus*. The type species of *Lissodus* (*L. africanus*) comes from a freshwater Karoo section (upper Beaufort Series) at Bekker's Kraal, South Africa (Brough 1935). The species from Angola has been assigned to *L. cassangensis* though other than the assemblage coming from a "freshwater environment" there is little information regarding the depositional environment.

The hybodont specimens found in Russia were previously assigned to *Hybodus*, though they are herein assigned to Hybodontiformes A and B. No specific information on the depositional setting ,was included with the original description (Minikh and Minikh 1985) though the area from which the specimens where found would suggest a continental freshwater origin. The specimens came from the Eastern European platform (the same general area as the Upper Permian Russian specimens), an area that was dominated by continental sections (Newell *et al.* 1999) and is known for its tetrapod finds (Tverdokhlebov *et al.* 2003). Marine sections where restricted to the Arctic regions (Benton, M.J. pers. comm. 2004). As previously stated the assignment of the specimens to *Hybodus* is tenuous as the material consists of isolated dorsal fin spines. To date there are no generally accepted diagnositic criteria for finspines in hybodonts (Cuny pers. comm. 2004). While undiagnostic, *Hybodus* specimens have been found in freshwater deposits (though not until the Cretaceous) (Cuny pers. comm. 2004)

5.4.4 Discussion

The data is too sparse to do any meaningful statistical analysis and at the 95% level all patterns for preferential survivorship are insignificant. Despite this the following

(very broad) patters can be seen. As Padian and Clemens (1985) suggested, sharks over the Permo-Triassic interval did tend to be found predominantly from marine deposits. In the Upper Permian only two areas yielded any freshwater shark specimens and the material is fairly poor and undiagnostic. Likewise in the Lower Triassic there are only three areas that yield freshwater shark fossils with none from the Induan.

There are four countries from which both Upper Permian and Lower Triassic remains have been found. Greenland, Germany and Japan all have sharks found from marine deposits on either side of the mass extinction event. With the exception of Germany (which has only one shark genus found from both the Upper Permian and Lower Triassic) the faunal turnover in marine sections is fairly striking. The Upper Permian Greenland fauna is dominated by large edestid genera with remains of only one hybodont genus. The Lower Triassic is a complete reversal with fossils from three hybodont genera but only one eugeneodont. Likewise in Japan, there are remains of several genera including two eugeneodont and a xenacanth from the Upper Permian but the Lower Triassic has only one hybodont shark.

It was previously thought that the Permian mass extinction caused the extinction of several purely marine shark groups, especially the eugeneodont and superficially they do seem to have been badly affected by the event, with only one out of five of the eugeneodont genera crossing the P-Tr boundary. Recent discoveries show that there are however far more Lower Triassic eugeneodonts than previously thought, with *Parahelicampodus* being found in the Induan of Greenland, at least one new (though undescribed) genus from Canada, *Helicampodus* from the Triassic of Armenia and fragmentary remains from Spitzbergen. This illustrates the relatively poor quality (due

either to a lack of study or poor depositional conditions) of the fossil record around the P-Tr boundary. Further evidence for the poor quality of the P-Tr fossil record come from the discovery of *Acrodus* specimens in the Lower Permian of the USA (Johnson 1981) and the Kungurian of Japan (Goto 2000) followed by an absence from the fossil record until they once again appear in the Olenekian of Spitzbergen and India.

There is only one area that has yielded both Upper Permian and Lower Triassic freshwater shark finds, Russia. The majority of the Russian sharks were hybodonts (though the exact generic assignment is in doubt). Even considering many of the original genera have not been accepted it can be seen that there was a substantial reduction in shark diversity in these freshwater sections. This area has been extensively sampled for tetrapods and it is believed the fossil record regarding this group is fairly accurate in the area (MJ Benton pers. com 2004) but this does not necessarily mean that the shark fossil record is equally good as sharks preserve far less frequently and have received relatively little study.

Over the P-Tr freshwater environments have an extremely poor quality fossil record. freshwater sharks such as xenacanths were also traditionally believed to have fared badly in the P-Tr extinction event as there are no xenacanths found in freshwater settings in the Lower Triassic. *Triodus* sp. was found from the Olenekian of India (Mehorta *et al.* 1991) but the authors claim it came from a marine environment. *Triodus* specimens from freshwater beds have however been found in the Middle and Upper Triassic of England, Australia and India (Johnson 1980). Johnson also postulates that *Triodus* (Johnson referred to them as *Xenacanthus,* but Hampe (2003) suggested all Triassic xenacanths should be assigned to *Triodus*) may have been present in South

America, Africa and Antarctica but that the size of the teeth and rarity of studied freshwater sites could have contributed to them not yet having been discovered.

There are too few specimens (especially freshwater ones) to do any meaningful statistical analysis. This, combined with the poor fossil record and relative lack of Upper Permian and Lower Triassic shark-yielding freshwater sites, make any conclusions drawn on the available information tenuous.

If we accept the generic assignment of the Russian specimens then it is possible to make some speculations. With the exception of *Helicampodus*, all of the genera identified from both the Upper Permian and Lower Triassic are capable of surviving in both marine and freshwater conditions. Xenacanths have previously been found in both marine and freshwater conditions implying that the specimen described as *Xenosynechodus* may have been capable of surviving in both. *Polyacrodus* and *Lissodus* were both found in freshwater conditions in the Upper Permian and were then subsequently found from marine deposits in the Lower Triassic. This may indicate a diversification into niches that were left open by other sharks following the mass extinction event. However it should also be noted that no freshwater sharks are found in the Lowest Triassic and only in the Olenekian are there finds of *Lissodus* from continental deposits. Hence it is equally possible that *Polyacrodus* and *Lissodus* where present (though as yet unfound) in marine settings in the Upper Permian (specimens of all three have been described from the Lower Permian), that they survived the Permian mass extinction in marine refugia and only subsequently recolonised freshwater settings indicating a preferential marine survival. This is however difficult to support as the lack of described Lower Triassic

freshwater sections make it possible that *Lissodus* and *Polyacrodus* were present in freshwater conditions during the Induan but have not yet been discovered.

As can be seen from the above, there is insufficient evidence to suggest that either marine or freshwater sharks were preferentially selected for in the P-Tr extinction event. It is clear from the large gaps between finds of genera such as *Acrodus* and *Triodus* that the quality of the fossil record surrounding the Permo-Triassic boundary is far too poor to draw any meaningful conclusion and that much more work needs to be done (especially in freshwater environments) before this issue can be resolved.

Chapter 6.

Concluding remarks

Despite the conclusions drawn in this work it is clear that more work needs to be done to fully understand the scope of the consequences on the P-Tr event of shark faunas. While several new specimens have been described in the work there are still far too few to build up a statistically viable sample set in many areas. To this end more field work needs to be done especially in areas such as Asia that have not benefited from the centuries of interest in palaeontology and corresponding sampling effort enjoyed by continents such as Europe and North America. In addition to this, collections of already discovered fossils, such as the eugeneodont collection in the University of Edmonton, need to be fully studied and described. Finally some of the lingering systematics issues such as fully resolving the genus *Hybodus* need to be addressed.

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